

THESIS: STUDIES IN THE GENERA
STERIPHOMA SPRENGEL, VALLEA MUTIS,
AND HARTIA DUNN.

by

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FIRST COPY



THE GENUS STERIPHOMA SPRENGEL.

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Distribution of the genera *Steriphoma* Sprengel,
Vallea Mutis and *Hartia* Dunn.

Taxonomic history of the Capparidaceae.

The Order has undergone numerous changes since its establishment by Bernard de Jussieu (1789). His Order *Capparidaceae* included true *Capparidaceae* genera such as *Stemodia* and *Capparis* and others which have since been removed to related families e.g. *Violes* and *Rubiaceae*. Later authors removed and added various other genera, increasing the general character of the group: for

THE GENUS STERIPHOMA SPRENGEL.

The genus *Steriphoma* belongs to the natural order Capparidaceae and is characterized by simple evergreen leaves, short terminal inflorescence, brilliant orange calyx, long protruding stamens and cylindric ovary on a long gynophore. In their natural habitat the species of the genus are woody shrubs growing to a height of about two metres.

Steriphoma is confined to the tropics of America. It occurs in South and Central America, having a longitudinal range of 20° north and south of the Equator and is recorded from the states of Venezuela, Columbia, Peru, Guatemala, the island of Trinidad and the isthmus of Panama. *S. elliptica* D.C. (Fig. 1) the species with which this work is concerned, occurs in Trinidad and Venezuela. *S. paradoxum* Endl. with which it is probably synonymous, occurs in Venezuela and Columbia.

Taxonomic history of the Capparidaceae.

The order has undergone numerous changes since its establishment by Bernard de Jussieu (1789). His Order Capparides included true Capparidaceous genera such as *Cleome* and *Capparis* and genera which have since been removed to related families e.g. *Viola* and *Reseda*. Later authors removed and added various other genera, increasing the general disorder of the group; for example, A. de Jussieu (1891) added such unrelated genera as *Drosera* and *Parnassia*. De Candolle (1824)

removed genera of doubtful affinity, retaining 17 genera, considered within modern generic limits. Endlicher (1836) divided 24 genera into two tribes, Cleomeae and Capparideae, on the basis of habit and fruit. Bentham and Hooker (1862) admitted 23, and Pax (1891) 34 genera.

The division of the Capparidaceae into two tribes has been continued throughout the taxonomic history of the family. The herbaceous Cleomeae with capsular fruit are separated from the arboreal or shrubby Cappareae with baccate or drupaceous fruit. The majority of the genera fall naturally into one or other of these groups.

The Capparidaceae are predominantly tropical, many genera being confined to the tropics or sub-tropics of America, Australia and Africa. A single herbaceous species, Cleome graveolens reaches Canada.

Taxonomic history of the genus Steriphoma.

The shrubby South American genus Steriphoma was given earliest mention by Loeffleur (1758) under the name Hermupoa. This description is unobtainable, the volume being in the original Linnaean library at Stockholm. Willdenow (1799) described the genus under the name Stephanina and Trattinck (1802) under the name Roemera. The generic name Steriphoma, which is now given precedence, was first used by Sprengel (1827) in the fourth edition of Linnaeus' 'Species Plantarum'.

Synonymy.

Seven species of *Steriphoma* have so far been described. Willdenow described the genus *Stephania* with a single species cleomoides (= paradoxum) evidently based on a plant "*Capparis paradoxa*" described and figured by Jacquin (1797) in his account of the Imperial Garden at Schoenbrunn. This plant, which came from the Caraccas (Venezuela) had "glabrous branches, lanceolate, acuminate, entire leaves, stellate-pubescent when young, and long petioles nearly as pubescent as the leaves". De Candolle (1824) added a second species elliptica, having "elliptical, scarcely acuminate leaves and petioles twice as long" (as those of S. cleomoides). These two species are thus distinguished solely by leaf shape and relative length of petiole, characters which are very variable even in the individual plant. Examination of Kew Herbarium specimens showed confusion in these characters. From all the evidence it appears that these two 'species' could well be regarded as synonymous.

Of the remaining five species two are distinct and three probably mere forms of S. elliptica. S. peruvianum Spruce (Eichler 1862) from Eastern Peru, is distinguished by a pubescent gynophore and S. Urbani Eggers (1898) from Manabi province, Ecuador, by its large white fragrant flowers. S. venezuelum Briquet (1913) resembles S. elliptica DC. from which it differs by a larger, glabrous leaf and deflected calyx.

S. macrantha Standley (1919) and S. clara Standley (1940) from Panama and Guatemala respectively, appear to have been named merely because of herbarium material from these localities. The descriptions indicate no characters differing from S. elliptica.

Uses and Cultivation.

Steriphoma appears to have no commercial or medical uses. It was introduced into Europe during the 18th century and has since been cultivated in hothouses in botanic gardens. "It grows well in a damp stone and strikes easily from cuttings", (Paxton 1853), reaching a height of one to two metres. It is surprising that it has not come into more general cultivation for the brilliant orange calyces and long curved filaments are very striking.

Material.

Material for this work was obtained from a plant of *Steriphoma elliptica* DC. growing in the hothouses of the Royal Botanic Garden, Edinburgh. A shrub about $1\frac{1}{2}$ metres high, it flowers regularly in June and July.

Methods.

Flowers, buds, leaves and young stems were fixed in Karpetschenko's and Carnoy's fluids, embedded in paraffin wax and sections of $6-12\mu$ thickness cut on a rotary microtome. Wood was softened by soaking in 50% glycerine-alcohol mixture and sections cut on a

sliding microtome. Petioles and small stems were sectioned by hand.

Various combinations of stains were used; gentian violet - Bismarck brown and gossypimine - picroeniline blue were the most useful. The iron-alum - haematoxylin procedure was used for young ovaries but was inferior to Bismarck brown for photographic purposes.

separate. STERIPHOMA ELLIPTICA DC. tube, alternating

Shrub, 1-2 m. high. Branches erect, slender, woody, covered with reddish-brown pubescence when young. Leaves evergreen, alternate, crowded toward end of branches, spreading and deflexed, lamina ovate or elliptic-oblong, rounded at base, acuminate, pubescent when young, 5-16 cm. long, 2-5 cm. broad; petiole slender, pubescent, swollen at junction with lamina and stem. Inflorescence terminal, racemose, short, dense-flowered. Pedicels orange pubescent, 2-4 cm. long; calyx tubular, brilliant orange pubescent outside, 1-5 cm. long, irregularly split into two or three lobes; petals five, narrow, spathulate, pale yellow, pubescent outside, 2 cm. long; stamens six, filaments slender, pale yellow, 4-6 cm. long, protruding horizontally beyond petals and curving upwards, anthers linear, 6 mm. long. Ovary on a long glabrous gynophore equalling length of stamens, cylindrical, dark-brown pubescent, stigma almost sessile. Fruit not seen, described as a cylindrical cortical berry about 10 cm. long; seeds numerous, angular, embedded in pulp.

(Text - Fig. 1c). Both calyx tube and petals contain

The Flower.

The ground-plant of the regular flower (Fig. 3) shows a calyx of four sepals (fused into a tabular calyx), four free petals, six stamens and a bilocular ovary of two fused carpels.

The tubular calyx is split on one side and is often notched where the tips of the component sepals and filaments are quite glabrous. The bases of the filaments are adnate to the gynophore for about three mm,

separate. At the base of the calyx tube, alternating with the petals, are four small nectary scales (see Text - Fig. 1b). The outer surface of the calyx is covered with a dense stellate pubescence, brilliant orange in colour, consisting of stalked and sessile hairs, which will be described later.

The calyx is undoubtedly composed of four fused sepals, by reason of (1) the presence of four nectary scales adnate to the base of the calyx tube and alternating with the petals, (2) the calyx tube has four main vascular strands, which alternate with the petals and (3) the split and notches in the calyx tube occur opposite a petal i.e. between two sepals.

The calyx has a simple internal structure of undifferentiated parenchyma and contains numerous small vascular strands in addition to the four main strands (see Fig. 4.)

The corolla. The four free, pale-yellow, narrow petals are slightly pubescent on the outer surface. Internal structure is again very simple. Each petal is supplied by a single branching vascular trace (Text - Fig. 1c). Both calyx tube and petals contain numerous secretory cells.

The androecium consists of six stamens, four being diagonally placed and two being orthogonal and lateral. The very long filaments are compactly coiled around the ovary in the bud (Fig. 5). Anthers and filaments are quite glabrous. The bases of the filaments are adnate to the gynophore for about three mm,

forming a short androgynophore. A single amphiploic vascular strand supplies each stamen.

The mature anther shows a normal internal structure (Fig. 6). Its most striking feature is the form of the epidermal cells which are greatly enlarged and papillate, except in the grooves between the anther lobes. Stomata are confined to the dorsal and ventral grooves. Small secretory cells are present in the connective. Surrounding each pollen sac are several compressed intermediate layers and an endothelial layer with narrow spiral bands of lignified thickening. Cells of the connective behind each pollen sac are also strengthened in this way.

The yellow pollen is produced in abundance but is not viable in the plant at Edinburgh. The grains are capable of germination but the pollen tubes soon degenerate.

The anther dehisces by two longitudinal slits. No definite stomium is present, but a narrow longitudinal strip of endothelial cells in the groove between each pair of pollen sacs are thin-walled and without strengthening bands. The contraction of the thin-walled epidermal cells on drying being greater than that of the strengthened endothecium, a tension results and a split occurs in the unstrengthened strip of tissue. The pollen sac walls spring outward and backward so dispersing the pollen. (Fig. 7).

The gynaecium. The ovary is borne on a slender

glabrous gynophore which is short in the bud but elongates rapidly in the opening flower until it carries the ovary beyond the anthers (Fig. 2.). This growth in length is due simply to a general increase in cell size and not to any meristematic activity. The stele is a simple cylinder of vascular tissue, (Fig. 8).

The cylindrical ovary is covered with a dense covering of dark brown stellate hairs. The very short style supports a flat stigma whose receptive upper surface is slightly four-lobed. In a young stigma the upper surface consists of cells drawn out into long papillae (Fig. 9). Immediately below this receptive layer lies a mass of elongate thin-walled cells, the conducting tissue, which passes into the centre of the style and into the placental column of the ovary. The conducting tissue is actually formed by the carpellary margins, the cells of which have become modified. (Capus 1878, Suegen 1901).

The vascular bundles in the style branch into a mass of short, wide, spirally-thickened tracheid endings (Fig. 10), which correspond in shape and structure to the 'water-storage' tracheids ('réservoirs vasiformes') described by Heinreicher (1885), Vesque (1882) and others. Their wide diameter and isodiametric form indicate a function other than that of conduction. Similar elements have been described in the stigma of certain species of Ericaceae by Pohl (1934) as modified terminal tracheids, and this is undoubtedly the case

in the stigma of *Steriphoma*. Storage tracheids have been recorded in the leaves of several *Capparis* species, where they represent modified parenchyma of the bundle sheaths, but none have so far been described in the stigma of a *Capparidaceous* flower.

The two carpels composing the ovary are situated anterior-posterior in relation to the floral axis, so that the two loculi are also anterior-posterior (see Fig. 3). Fusion of the carpels is complete in the mature ovary. In a very young ovary the carpel margins project into the ovarian cavity but are not yet fused (Fig. 18).

In the possession of a bilocular ovary *Steriphoma* differs from the majority of *Capparidaceous* genera which have unilocular ovaries. The axile state, however, is but one step removed from the parietal, being due simply to fusion of the fertile carpel margins, and the derivation of one from the other is easily followed in transverse sections of young ovaries at successive stages of development.

Placentation in the ovary is axile, the ovules being borne on the central column formed by the fused carpel margins, superposed in four rows. The ovules of one row alternate in level with those of the adjacent row (Fig. 11).

Numerous flowers on the plant from which material was obtained contain very small ovaries which remain almost sessile in the open flower as the very short gynophore does not elongate. Such flowers are

functionally unisexual, the ovaries being completely sterile. A transverse section of such an ovary (Fig. 12), shows a hollow placental column and degenerating ovules, which never develop beyond the archesporial stage. The ovaries which did mature never set seed, and it is doubtful whether fertilization ever occurs.

The ovules are of the campylotropous type characteristic among Capparidaceae (see Text - Fig. 71). The outer integument consists of two layers, the inner of three or four. Nucellus tissue is abundant and the embryo sac relatively small. Orr (1921) recorded the occurrence of tracheid-like elements within the nucellus of the ovules of Steriphoma cleomoides - "They are particularly obvious in sections stained with gentian-violet". Careful examination of sections of S. elliptica ovaries revealed short, spirally-thickened elements near the embryo sac of a few ovules (Fig. 13). They are not connected to the vascular strand of the funicle. The presence of these elements in the ovules of Steriphoma is curious as they have not been noted in other genera of Capparidaceae and in fact have so far been recorded only three times - in the nucellus of Casuarina species (Treub 1891), in Castanea vulgaris (Benson 1894) and in Asclepias cornuta (Frye 1902).

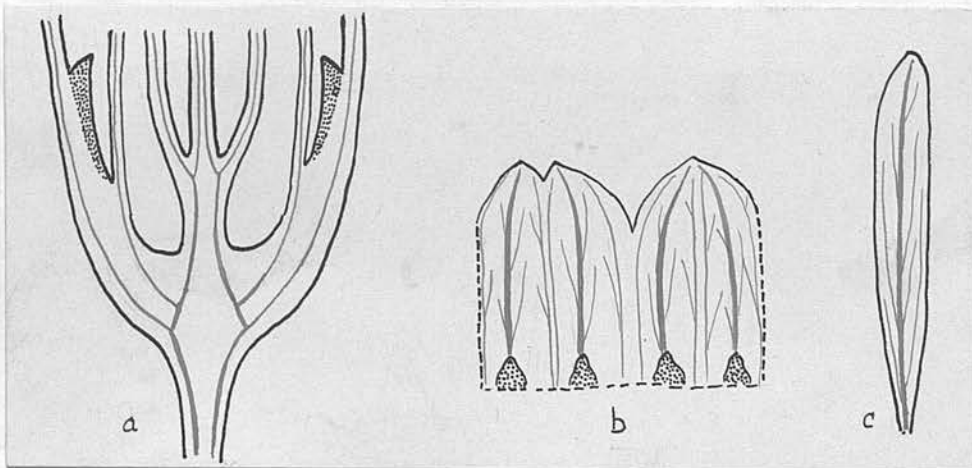
Secretory elements are more abundant in the gynoecium than in any other part of the plant; they are present in style, stigma and ovary walls but not

within the ovules or placental column. Stomata are numerous in both inner and outer walls of the ovary. They were observed in the inner ovarian wall of Cleome spinosa and Isomeris arborea by Orr (1921) but Raghaven (1937) did not find them present in Cleome chelidonii.

Fruit and Seed.

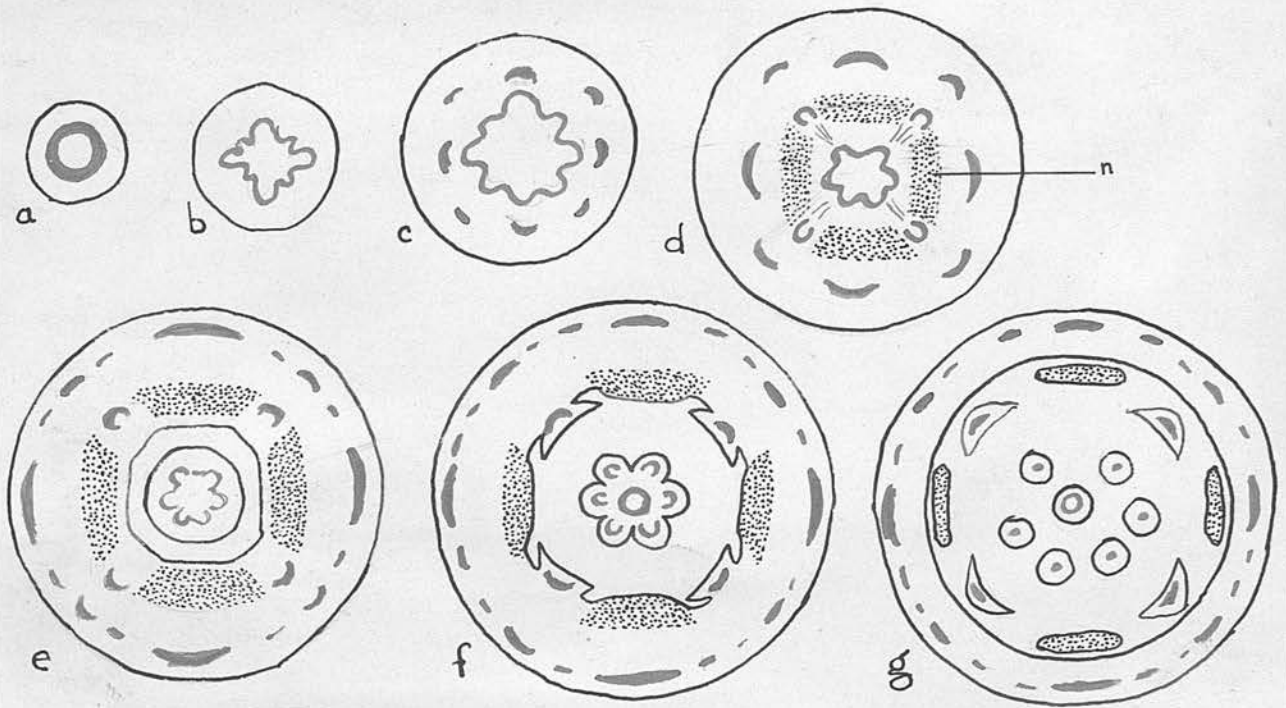
Under natural conditions the ovary matures into a cylindrical, indehiscent berry, pendulous on the long gynophore, with a thick rind and pulpy interior in which numerous seeds are embedded. According to Eichler (1862) the fruit is "about the thickness of a thumb". Williams (1929) states that "the berry is 10 cm. or more in length, 3-5 cm. broad, with a rind about 5 mm. in thickness". Fruit and seed are figured by Planchon (1850). The seed is reniform, non-endospermic; the embryo has two spirally-convoluted cotyledons (Endlicher 1836).

Vascular Anatomy of the Flower.



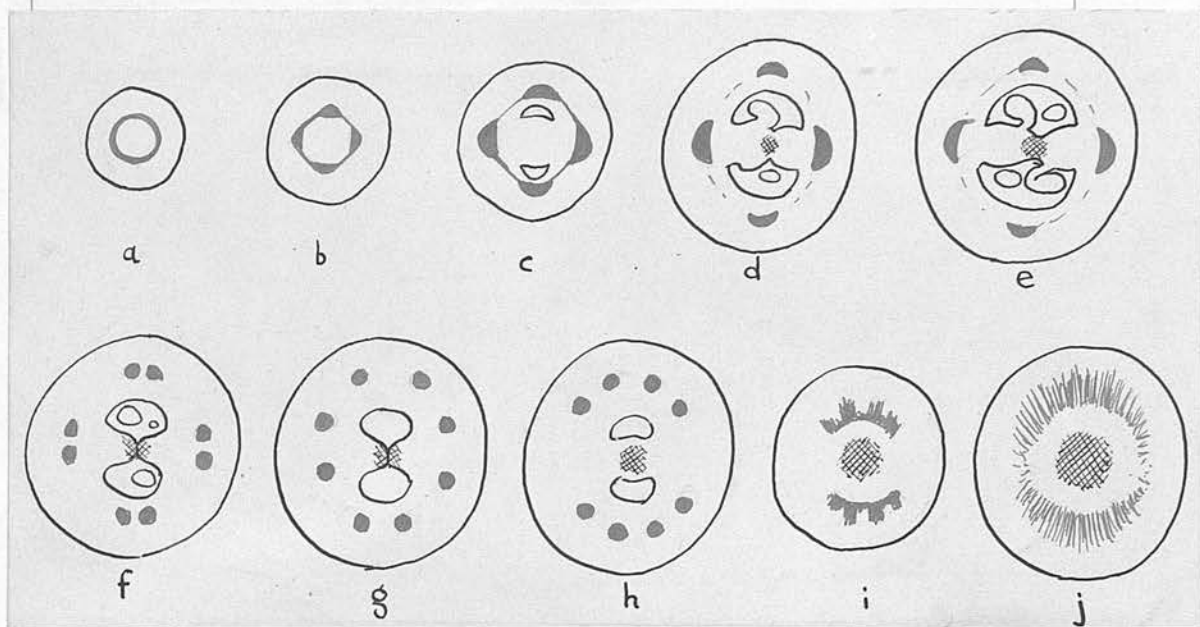
Text - Fig. 1. Vascular Anatomy of flower. Diagram

- (a) vertical section
- (b) Calyx cut open and spread out
- (c) petal.



Text - Fig. 2. Vascular Anatomy of torus. Diagram.

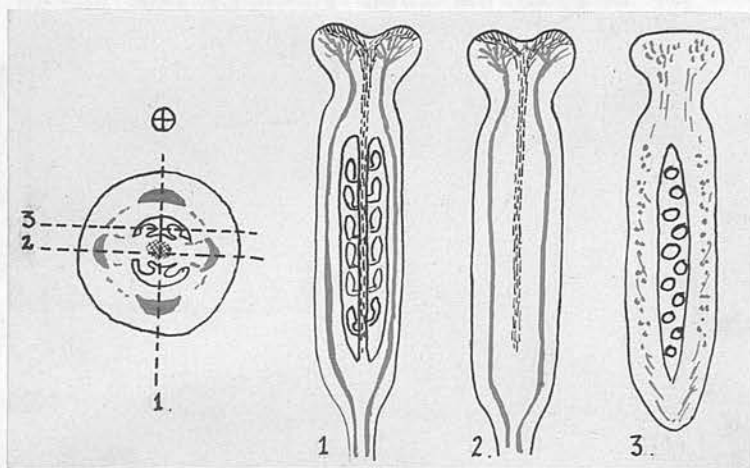
The pedicel shows in T.S. (Text - Fig. 2A) a ring of secondary wood. On entering the base of the torus the vascular cylinder becomes convoluted (2b) and eight traces separate to the calyx (2c). Four diagonal traces are then given off to the petals (2d). The glandular tissue of the nectary scales (n) at the base of the calyx becomes apparent at this level. The convoluted central stele now gives rise to six curved stamen traces (2e). The fused bases of calyx and corolla now separate from the fused gynophore and filaments (androgynophore). When the filaments separate (2f, g) a single strand runs into each filament, the remaining cylinder of vascular tissue continuing up the gynophore to the ovary. (Text - Fig. 3a).



Text - Fig. 3. Vascular system of ovary. Diagram.

On entering the base of the ovary the vascular tissue becomes concentrated into four strands (3b) which separate as the ovarian loculi appear (3c). The two lateral strands become prominent while the two median strands become smaller (3d). The former are the fused marginal strands of the two carpels, the latter are the dorsal or 'midrib' carpellary strands. Small bundles connect the dorsal with the fused marginal strands and run from the latter into the central column to supply the ovules. This is the condition up the length of the ovary (3e). Near the apex of the ovary the lateral strands each split into two (the marginal strands); the dorsals also divide (3f) and the eight strands thus formed move apart (3g). At the extreme apex of the ovary these strands aggregate into two groups, each consisting of a split dorsal and two marginal strands (3h). In the short style the strands compact (3i) then spread

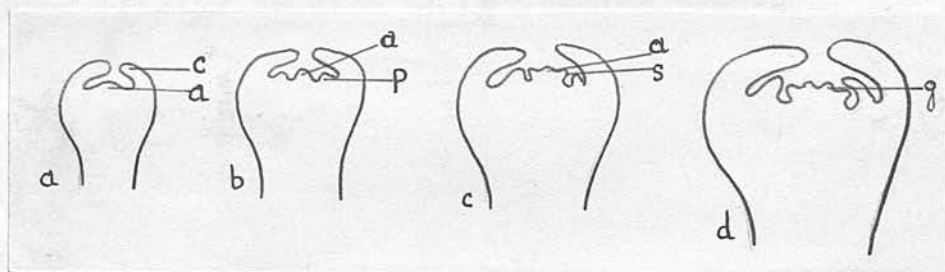
out and separate into a mass of enlarged tracheid endings (3j).



Text - Fig. 4. Vascular system of ovary in different planes of section. Diagram.

The appearance of the ovarian vascular system differs according to the plane of section, as is shown in Text - Fig. 4.

Ontogeny of the Flower.



Text - Fig. 5. Stages in development of Flower. L.S. Diagram.

a = floral apex
s = stamen primordium
g = carpel primordium

c = calyx primordium
p = petal primordium

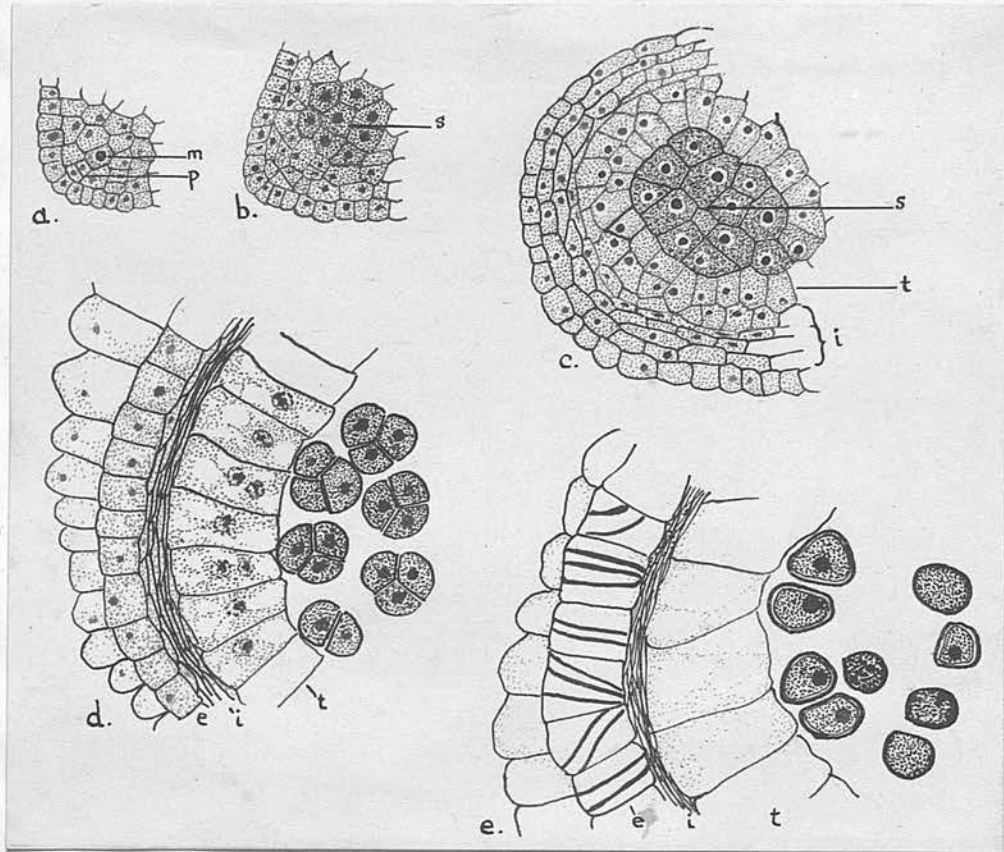
The flower initial arises as a small rounded protuberance in the axil of a bract (Fig. 14). The sepal primordia arise first and are coalesced into a calyx tube from the time of their initiation. The

tube arches over until its edges touch, thus enclosing the floral apex (Fig. 14, Text - Fig. 5a). Multicellular hairs are already well developed on its outer surface.

The other floral whorls arise in acropetal succession after the calyx tube has been initiated. The petals arise as small protuberances just below the floral apex which broadens out so that, in section, the petal primordia appear level with it (5b). The stamen primordia are next initiated around the broad floral apex (5c). Fig. 15 shows a section of a bud at this stage of development; the section is not quite median so that the calyx tube appears fused at the top. Lastly, the floral apex becomes apparently two-lobed, the lobes being the two carpel primordia which arise laterally and rapidly fuse by their incurved margins to give an unilocular ovary.

Ontogeny of the Stamen.

The stamen primordium is at first a homogeneous mass of small meristematic cells. The uppermost portion which is going to form the anther soon becomes slightly four-lobed in transverse section (Fig.16). An archesporial cell differentiates in the hypodermal layer under each lobe and divides periclinally to give a parietal cell and a microspore mother cell (Text-Fig.6a). The former divides repeatedly to give several parietal layers, the latter to give a mass of sporogenous or 'pollen mother-cells' (Fig.17, Text-Fig.6b), which separate and divide meiotically to give spore tetrads (6d)



Text-Fig. 6. Stages in development of microsporangium.

m	microspore mother cell	p	parietal cell
s	sporogenous cells	t	tapetum
i	intermediate layers	e	endothecium

The innermost parietal layer differentiates into a nutritive tapetum of large, radially-elongated cells with prominent nuclei and vacuolated cell contents (6d).

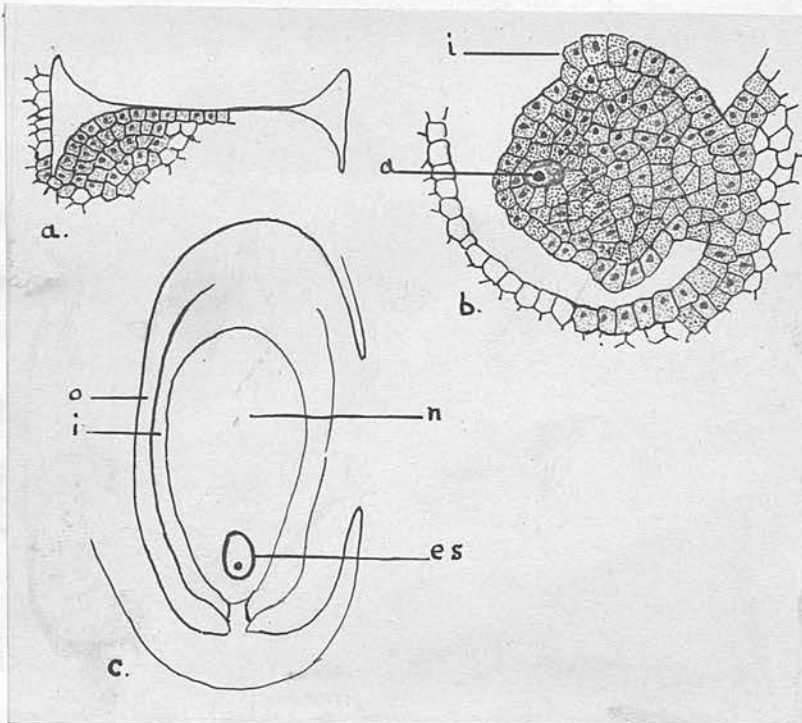
The outermost parietal layer differentiates into an endothecium by enlargement, radial elongation, and the deposition of radial and spiral bands of lignified thickening upon the walls of the cells. The endothecium is not fully developed until the pollen grains have separated from the tetrads and rounded off. By this stage the tapetum has completed

its nutritive function

and appears empty.

The remaining parietal layers (intermediate layers) are crushed tangentially between the enlarging endothecium and tapetum until little remains of them save crushed cell walls.

Ontogeny of Ovule.



Text - Fig. 7. Stages in development of Ovule.
X250 (a, b) X100 (c).

p = ovule primordium	a = archesporial cell
i = inner integument	n = nucellus
o = outer integument	es = embryo sac.

Before the carpel margins meet and fuse in the centre of the very young ovary, numerous slight protuberances, formed by cell division in the underlying layers, appear in the carpel epidermis in four longitudinal rows. These are the ovule primordia (Fig. 18, Text - Fig. 7a). As the carpel margins grow together in the centre of the ovary the ovule primordia enlarge

and project into the ovarian cavities. An annular ridge appears in the epidermis near the base of the young ovule - this will form the inner integument (7b). A second ridge, the outer integument, appears slightly later, but its growth being more rapid it soon overtakes the inner integument.

The archesporium is initiated by a hypodermal cell (at about the same time as the initiation of the first integument) which enlarges and shows a prominent nucleus (7b). By division this archesporial cell gives rise to several parietal cells and a megaspore mother-cell.

Further development follows the normal course. The ovule is originally orthotropous (see Fig. 11) but during development the whole body of the ovule curves away from the centre of the ovary to face the side wall, thus becoming campylotropous (6c). According to Raghaven (1937) the campylotropous curvature so characteristic of the ovules of Capparidaceae is attained only after fertilization, but this is certainly not the case in *Steriphoma*.

Hairs.

Multicellular hairs of characteristic structure occur in greater or less density over the lamina, petiole, young stems, calyx, corolla and ovary. No unicellular hairs occur. The form of these hairs is peculiar to the genus *Steriphoma* among the Capparidaceae.

The hairs are of two types - peltate and sessile,

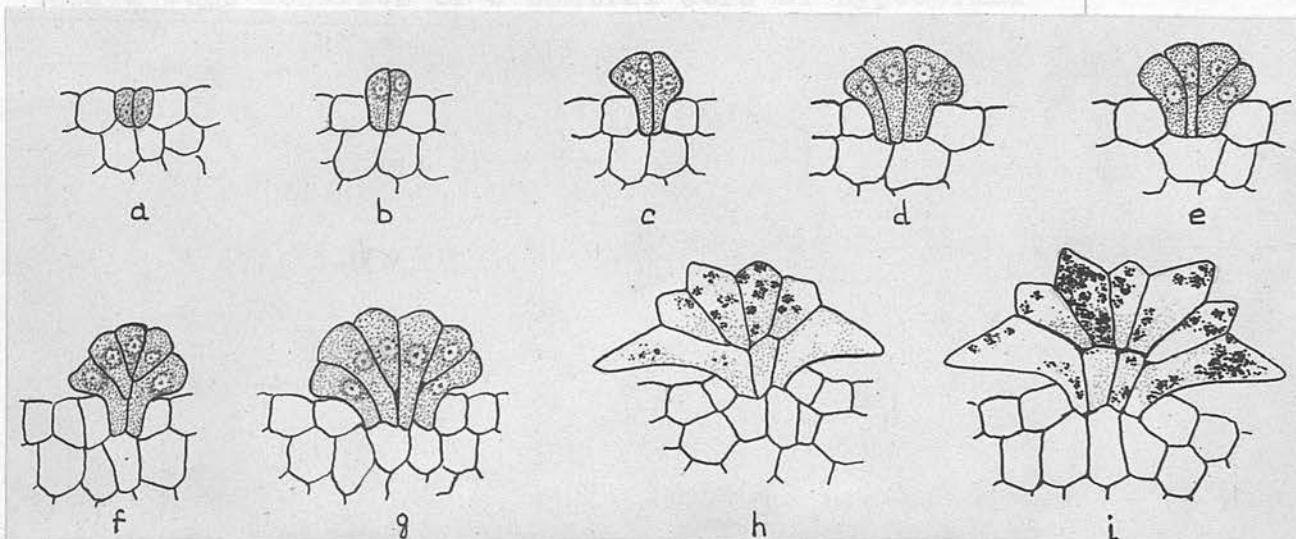
the latter being the most numerous. When viewed from above (Fig. 20) both types show several to many elongate tapering cells, "ray" cells, radiating from below a central cluster of smaller cells ("top" cells). Viewed laterally, the peltate hairs are seen to be raised above the epidermis by a columnar stalk of several cell layers.

The leaf shows both peltate and sessile hairs, the cells of which are colourless and apparently empty. The ray cells are longer and narrower than those of hairs or other parts of the plant, and the top cells smaller in comparison (Fig. 22).

The petiole, young stems, perianth and ovary bear peltate and sessile hairs containing a clear yellow substance which readily absorbs stains and is present as granules of various size or completely fills the cell cavity. The ray cells are shorter and broader than those of the leaf hairs (Fig. 20b, c, d,). Fig. 19 which is a microphotograph of an unstained preparation of the calyx taken by transmitted light, shows that the substance in the hairs absorbs light. Vesque (1882) noted the presence of this yellow substance in the hairs of *Steriphoma* and concluded that they were glandular in nature. The substance is undoubtedly secretory but its function is difficult to understand. The possession of such hairs is a characteristic which *Steriphoma* shares with the herbaceous *Cleomeae*, in which they are of frequent occurrence in contrast to the aboreal *Cappareae* among which they occur more rarely.

The ray cells radiating in one plane and the presence of smaller top cells or "upper scales" give the hairs of *Steriphoma* a position intermediate^{to} the small peltate scales so frequent among *Capparidaceae* and the brush-like type of stellate hairs observed only in certain species of *Capparis*.

Development of hairs is most easily followed in sections of the young ovary.



Text - Fig. 8. Stages in development of
sessile hairs. X250

The first stage in the development of a hair is the anticlinal division of an epidermal cell into two equal cells (Text- Fig. 8a) which elongate and project above the surface of the epidermis (8b). The projecting portions enlarge (8c) and longitudinal division gives a four-cell stage (8e). Often one cell divides before the other giving a three-cell stage (8d).

Division continues unevenly so that the resulting cells are of unequal size, the smaller cell becoming a 'top' the larger a 'ray' cell (8 f, g,).

In the case of a sessile hair there may be a slight enlargement of the hypodermal cells immediately below the hair but no further cell division takes place (8h, i). The stalk of a peltate hair is formed by transverse division in the hypodermal cells immediately below the ray cells followed by division in the adjacent epidermal cells. The new cells thus formed raise the cap of ray cells above the epidermis. The mature stalk thus consists of a central core of hypodermal cells surrounded by a single layer of epidermal cells. This is well shown in Fig. 21b.

As the hairs mature their cells lose their nuclei and dense protoplasmic contents. Small granules or droplets of a darkly-staining substance appear in the ray and top cells (8f, g) and gradually enlarge and coalesce until they may eventually fill the cells completely; this is especially so in hairs on the ovary (Fig. 21a, b). The substance does not appear in the stalk of peltate hairs nor in hairs on the leaf.

The development of the peltate hairs of *Steriphoma* is similar to that described for those of *Shepherdia canadensis* and other species of *Eleagnaceae* by Cooper (1932) in that the 'cap' of ray cells develops from a single epidermal cell and the stalk from both hypodermal and epidermal cells. It differs from that described for similar hairs in other families by other authors. Prillieux (1856), for example, found that the peltate hairs of *Oleaceae* develop from a single epidermal cell which divides horizontally, to form an

upper and a lower cell; the cap develops from the upper and the stalk from the lower cell. Groenland (1855) noted a similar development of the glandular peltate hairs of *Pinguicula*.

Secretory Elements.

Secretory elements occur throughout the leaf, petiole, cortex, phloem and pith of stem and root, and in the reproductive organs, being especially abundant in the ovary walls. The elements sometimes are in the form of the cells of the tissue in which they are found, as in the palisade and mesophyll of the leaf, though they may be larger than the normal cells (see Figs. 25, 26, and 27). In the stem they occur as vertically elongated, narrow elements, sometimes divided into two or three parts. Their contents, which may or may not fill the cell cavity, stain densely and react to Millon's reagent.

Internal secretory cells are general throughout the Capparidaceae. Vesque (1882) described "mucilage-cells" in leaf and petiole of certain species, but not in the two species of *Steriphoma* whose leaf he described (*S. paradoxum* Endl., *S. peruvianum* Spruce). The proteid nature of the contents of these secretory elements is shown by their reaction to Millon's reagent. In this and also morphologically they resemble the special secretory cells of Cruciferae, named "Myrosin cells" by Guignard (1893). Heinricher (1886) described them

in the leaf and stem of several Capparis species and named them "proteid sacs" because of the nature of their contents.

The function of these proteid-secreting cells is unknown; they must serve some physiological purpose but whether it is secretory or merely excretory remains doubtful.

The Leaf.

The lamina. Peltate and sessile hairs occur on both surfaces. In all respects the structure of the lamina is that of a normal dorsiventral dicotyledonous leaf. The upper epidermis (Fig. 23) is covered with a thin cuticle; the cells are rather large, isodiametric and usually pentagonal in surface outline.

Palisade and spongy mesophyll each occupy half the thickness of the mesophyll tissue. The palisade is single-layered, the cells being closely packed with small intercellular spaces, and includes numerous secretory cells (Figs. 25, 27). The spongy mesophyll consists of loose parenchyma with large intercellular spaces. Secretory cells are less frequent than in the palisade (Fig. 26).

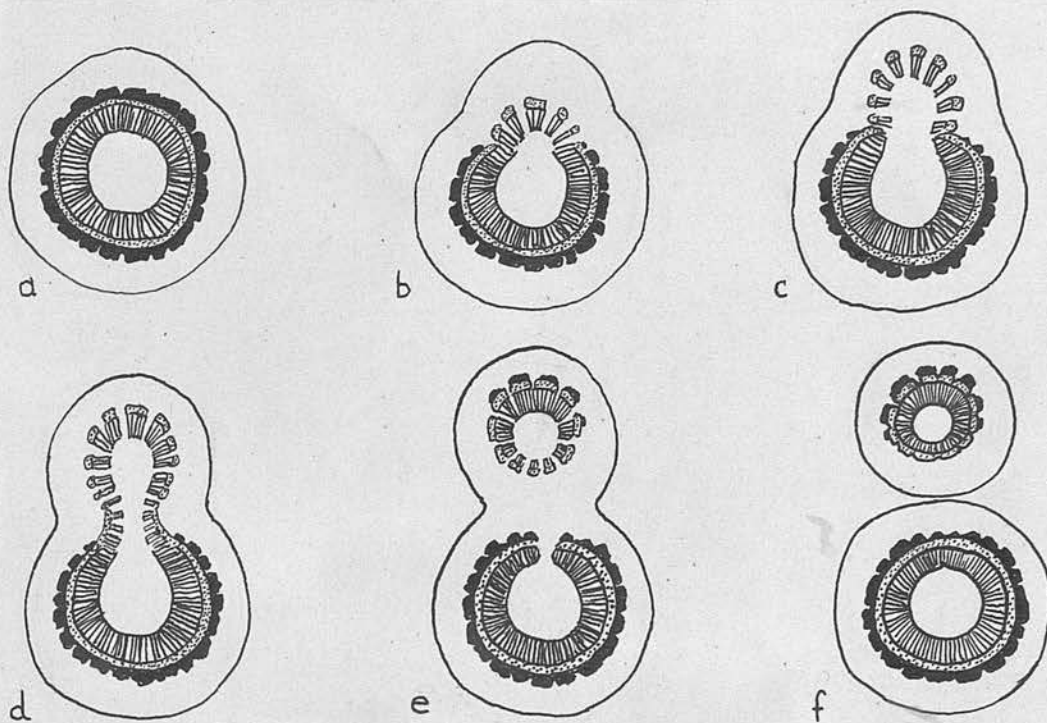
The lower epidermis consists of smaller, more irregularly shaped cells than does the upper epidermis. Stomata are very numerous (about 140,000 per sq. cm. of surface) and show no special subsidiary cells. The guard cells are small, $10-12\mu$ in length, $6-8\mu$ in width with a pore 6μ long.

Features such as spicular cells, crystals and papillose epidermis which occur in some Cappariaceae are not present in the leaf of Steriphoma.

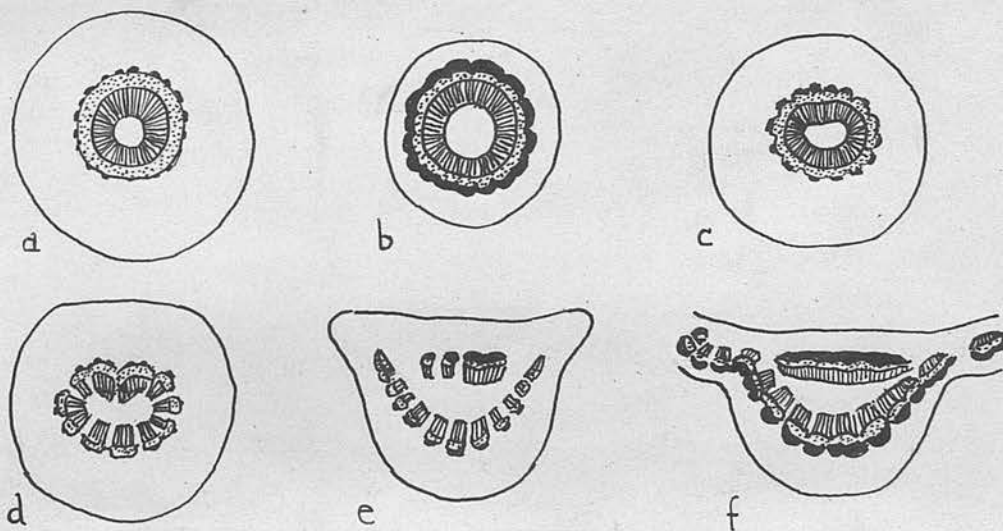
The midrib contains 8-10 xylem-phloem bundles in an upward curving arc; a small arc is inversely orientated above it. There is a slight collenchymatous thickening of the tissue below and above the vascular strand. At the base of the midrib the strand is enclosed by a more or less complete sheath of fibres and stone cells: this gradually disappears up the midrib. The lateral veins consist simply of a xylem-phloem strand traversing the mesophyll, devoid of any sclerenchymatous sheath.

The petiole is swollen into a pulvinus at its junction with the stem and an articulus at its junction with the midrib (see Text - Fig. 10), and is covered with multicellular hairs. The cortex contains numerous secretory cells (Fig. 28). A pericyclic ring of sclerosed fibres surrounds the vascular strand along the greater length of the petiole.

The leaf trace is given off from the stele (Text-Fig. 9a) as a phloem-xylem arc (9b) which passes through the cortex of the stem (9c, d) and closes into a complete cylinder in the swollen pulvinus of the petiole (9, f). Small groups of sclerenchyma fibres appear outside the phloem groups (9e) and enlarge until they form a sheath around the vascular strand (Text-Fig. 10a, b, c), disappearing as the strand enters the articulus.

Text-Fig. 9.Leaf trace diagram.

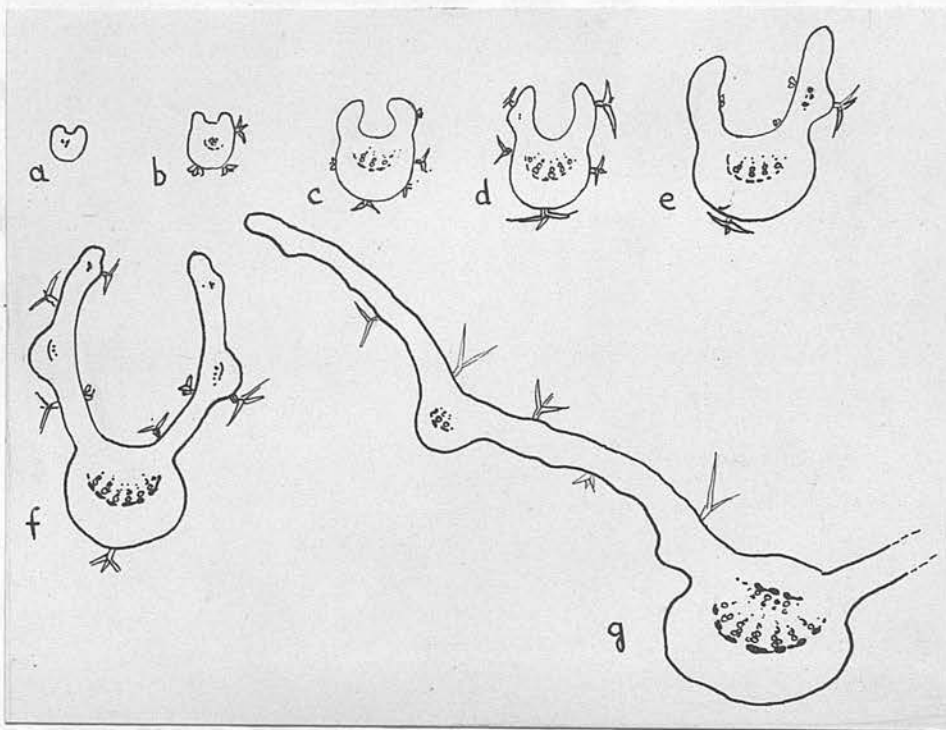
Here the cylinder breaks up into numerous small strands (lod). A break occurs in the uppermost side and the two edges curve inwards and join to form a small inversely orientated arc.

Text-Fig. 10.Petiole vascular system diagram.

Ontogeny of the leaf.

The leaf initials arise close behind the stem apex in the promeristematic area. Hairs are already

well-developed on their outer (abaxial) surface (Fig. 34). The initials are rounded protuberances which rapidly elongate and develop two parallel ridges on their inner (adaxial) side, (except at the base which will form the petiole). These are the marginal meristems which produce the two sides of the leaf blade (Fig. 19). The tip of the leaf initial remains meristematic and is responsible for growth in length. Text- Fig. 11 shows the relative sizes of midrib and lamina in successive stages of growth of the young leaf.



Text - Fig. 11. Stages in Leaf growth. X 25.

At the stage of development shown in Text - Fig. 11f and Fig. 32, the hypodermal cell layer begins to elongate and differentiate into the palisade (see also Fig. 30); the mesophyll is still compact tissue with no intercellular spaces. By this stage hairs are developing on the upper (adaxial) surface of the young leaf.

Protovascular elements are evident in the very young leaf (Fig. 31). Secondary vascular increase occurs in older leaves and petiole by cambial activity.

The Stem.

The vegetative stem grows in length by an apical meristem - a mass of rapidly-dividing cells immediately behind the apex. Interpreted by the "tunica-corpus" theory of the stem tips of vascular plants, the stem apex shows a single outer layer of cells which divide only in an anticlinal direction (the 'tunica') enclosing an inner mass of cells dividing in all planes (the 'corpus').

Leaf initials arise as rounded protuberances immediately behind the stem apex (Figs. 33 and 34). A small area at the base of the leaf initial remains meristematic and produces a bud in the leaf axil.

Behind the apex of undifferentiated promeristematic tissue the young stem rapidly becomes differentiated into the primary tissue - dermatogen, periblem, plerome - which soon become the permanent primary tissues (epidermis, cortex, stele). About 2 mm. behind the stem tip a transverse section shows an outermost layer or dermatogen, a periblem area of about ten cell layers, a ring of small groups of meristematic procambial cells and a large pith, the cells of which are still dividing. Certain pith cells differentiate into secretory elements (see Fig. 34).

Small groups of protoxylem are formed by the

procambial cells which later also form protoxylem to the inside of the stem. In a young stem 3 mm. behind the tip the epidermal, cortical and stelar areas are well differentiated. An almost complete ring of vascular tissue is formed by numerous small phloem-xylem groups hardly distinct enough to merit the name of 'vascular bundle'. Further behind the apex a small group of cells external to each phloem group differentiate into hard cortical fibres by the deposition of lignin on the walls, which become greatly thickened (Fig. 35).

Secondary growth begins early, and stems of only 3 mm. diameter may have a distinct zone of secondary wood. Secondary growth follows the normal dicotyledonous pattern. The cambium cuts off radial series of xylem prosenchyma, with an occasional vessel, toward the pith, and secondary phloem to the outside of the stem. Lignified pericyclic fibres form an almost complete ring of mechanical tissue immediately external to the phloem (Fig. 36).

Cork formation begins in the outermost cortical layers from a cork cambium which cuts off regular rows of rectangular cork cells to the outside. The outer layers of the primary cortex become ruptured owing to the increase in volume of the secondary xylem and are sloughed off.

The bark is largely occupied by secondary phloem whose bands of sclereids and fibres are its most obvious feature (Fig. 37). It consists of narrow

tangential bands of sieve tubes, companion cells and parenchyma separated by bands of hard sclereids and bast fibres, the whole traversed radially by uniseriate medullary rays. Elongated secretory elements occur scattered throughout the secondary phloem.

The wood is hard and of a very compact texture due to the vessels being small and relatively few in comparison with prosenchyma and lignified parenchyma (Fig. 38). Medullary rays are numerous and uniseriate. Annual rings^{are} indistinguishable in wood from the plant at Edinburgh, due no doubt to the artificial conditions under which it grows. The ringed appearance in transverse section (Fig. 38) is due to bands of lightly-staining xylem parenchyma. In L.T.S. the parenchyma elements can be distinguished from the prosenchyma elements by the presence of internal septa; otherwise there is little difference apart from differential staining. Both have tapering ends and vary in size between the same limits.

The vessels occur singly or in short radial series (see Fig. 39); they are circular or slightly oval in cross-section and vary in diameter from 20-50 μ . The vessel segments are short (about 500 μ) and the numerous septa horizontal or slightly oblique (Fig. 40). Bordered pits on the vessel walls are circular to oval in surface outline; no scalariform pitting was observed.

The prosenchyma forms the main volume of the wood. The elements are small, angular in cross-section, with

tapering ends and from 100-200 μ in vertical length.

Xylem parenchyma as noted above, is similar to the prosenchyma but the elements are septate and stain more densely.

Medullary rays are uniseriate and extend radially across two to many rings of growth. In vertical depth they vary from two to twenty cells (Fig. 41). The cells are rectangular in transverse section. Simple pits occur on all walls.

Starch granules are present in the medullary rays and in some prosenchyma elements (see Fig. 40). The granules are large, stain, dark-blue with iodine and have a central black speck.

The root wood is of very compact texture; vessels are fewer than in the stem wood, which is an unusual feature. Xylem parenchyma is again present in narrow bands (Fig. 42). Starch is present in great abundance in prosenchyma, parenchyma and medullary rays (Fig. 43).

Steriphomia in the structure of its peltate hairs which have a small upper scale equivalent to the 'top' cells of the peltate hairs of *Steriphomia*. These two genera are unique among *Cyperidaceae* in possessing this type of hair. The presence of an inversely orientated area of vascular tissue in the midrib is a feature of *Steriphomia* which *Marionia* shares with several other genera.

Secondary structure in the *Cyperidaceae* has so far received comparatively little attention so that a comparison of the secondary anatomy of *Steriphomia* with

Discussion.

The genus *Steriphoma* falls naturally into the Capparideae group of the Capparidaceae by reason of its woody growth and many-seeded, baccaceous fruit. It shows a similarity, however, with the herbaceous Cleomeae in the possession of glandular hairs, which are of frequent occurrence in the latter group and occur only rarely in the Capparideae.

Floristically, *Steriphoma* most closely resembles the genus *Morisonia* Linn, which has a similar distribution in tropical America and which differs chiefly in its campanulate or funnel-shaped calyx, stamens shorter than the petals and globose fruit.

The great diversity of anatomical structure prevailing among the Capparidaceae renders anatomical characters of little use in generic diagnosis. Some, such as leaf structure, are useful for distinguishing species. *Morisonia*, however, shows a marked resemblance to *Steriphoma* in the structure of its peltate hairs which have a small upper scale equivalent to the 'top' cells of the peltate hairs of *Steriphoma*. These two genera are unique among Capparidaceae in possessing this type of hair. The presence of an inversely-orientated arc of vascular tissue in the midrib is a feature of *Steriphoma* which *Morisonia* shares with several other genera.

Secondary structure in the Capparidaceae has so far received comparatively little attention so that a comparison of the secondary anatomy of *Steriphoma* with

that of other genera is not possible. Solereder (1908) states that in the genera *Capparis* and *Crataeva* the medullary rays of the wood are multiseriate - this contrasts with the uniseriate rays found in *Steriphoma*, but otherwise the main features of the wood are similar.

Anomalous stem structure has been observed in several genera in the form of successive rings of growth. *Steriphoma*, however, shows no evidence of anomalous structure in either stem or root.

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STERIPHOMA ELLIPTICA DC.

FIGURES.

Fig. 1 Inflorescence. X $\frac{1}{2}$.

Fig. 2 Flower. Vertical section X 2.

(a) normal bisexual flower

 ag androgynophore

(b) functionally male flower with small
 sterile ovary.



Fig. 1

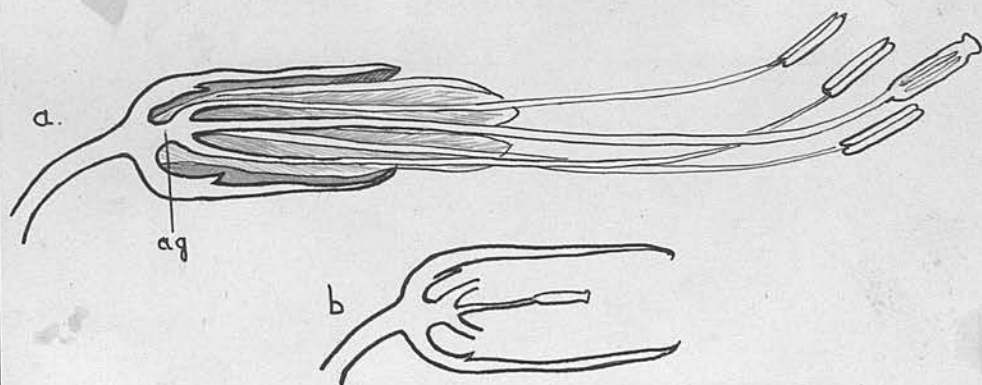


Fig. 2

Fig. 3 Floral diagram.

Fig. 4 Flower bud. T.S. at anther level X 40.
showing numerous vascular strands in the
calyx.

Fig. 5 Flower bud with perianth removed X 2
showing contortion of the stamen filaments.

Fig. 6 Anther at tetrad stage T.S. X 50
Note the enlarged epidermal cells.

Fig. 7 Dehiscent anther. T.S. X 50.

Fig. 8 Gynophore. T.S. X 40.

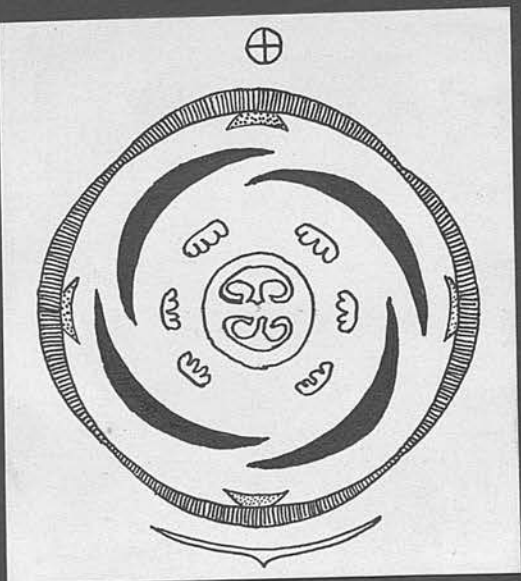


Fig. 3

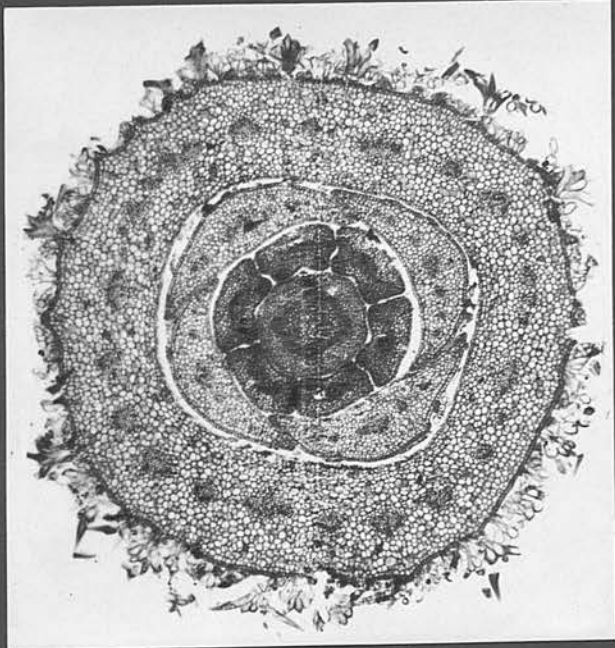


Fig. 4



Fig. 5

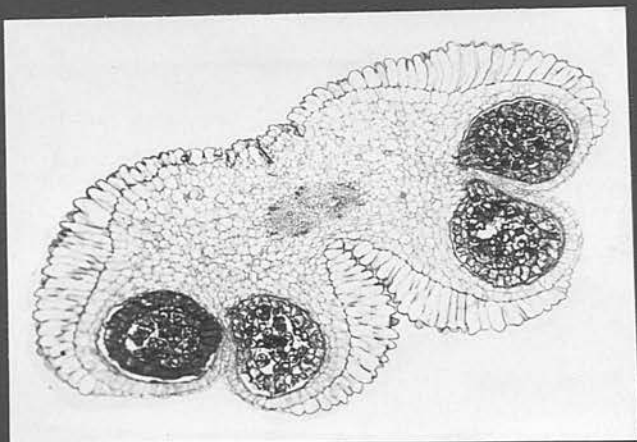


Fig. 6

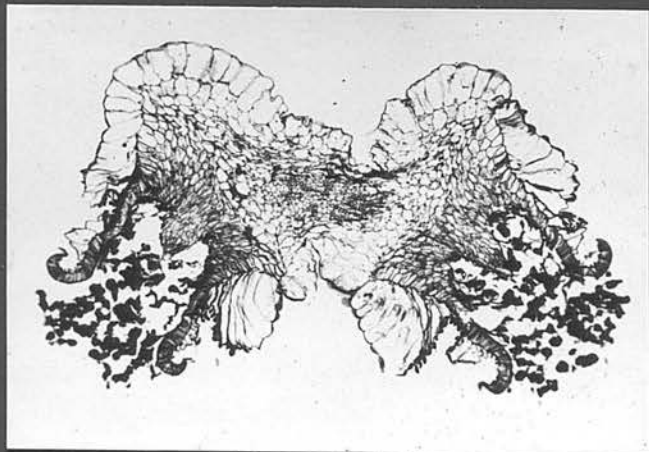


Fig. 7

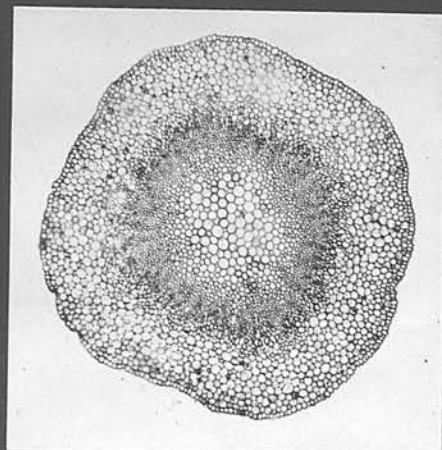


Fig. 8

Fig. 9 Stigma. L.S. X 25.

Fig. 10 Tracheid endings in stigma. L.S. X 40.

Fig. 11 Young fertile ovary. T.S. X 40

showing axile placentation of the ovules
and development of multicellular hairs on
the outer surface.

Fig. 12 Sterile ovary. T.S. X 40.

showing degeneration of the placental column
and abortion of the ovules.

Fig. 13 Tracheids in nucellus (diagrammatic). X 25.

Fig. 14 Young inflorescence. L.S. X 25.

i flower initial
c calyx primordium
b bract

Fig. 15 Young flower bud. L.S. X 55.

The section is slightly oblique so that the
calyx appears fused at the top.

c calyx
a floral apex
s stamen primordium
p petal primordium

Fig. 16 Very young anther. T.S. X 100.

Fig. 17 Young anther. T.S. X 100.

s sporogenous cells

Fig. 18 Very young ovary. T.S. X 150.

showing the carpel margins meeting in centre
Of ovarian cavity but not yet fused.

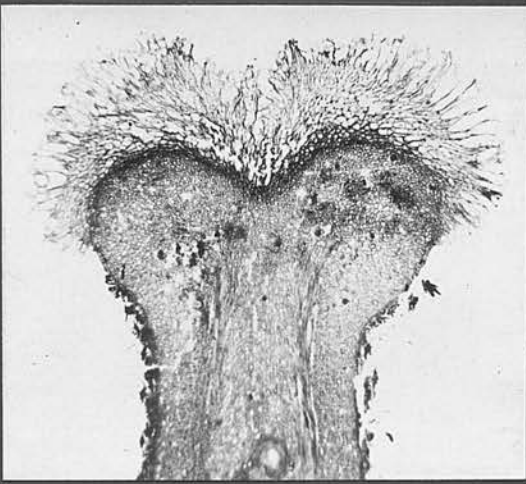


Fig. 9

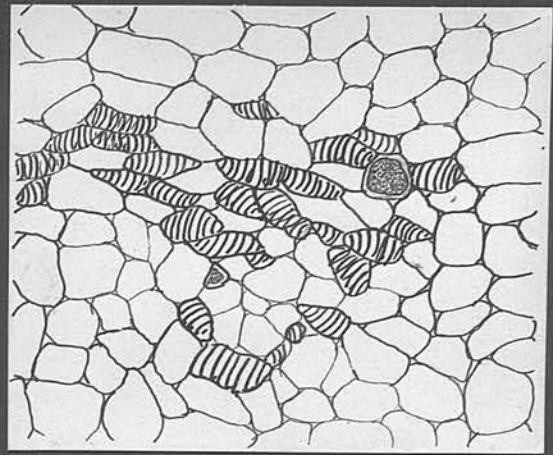


Fig. 10

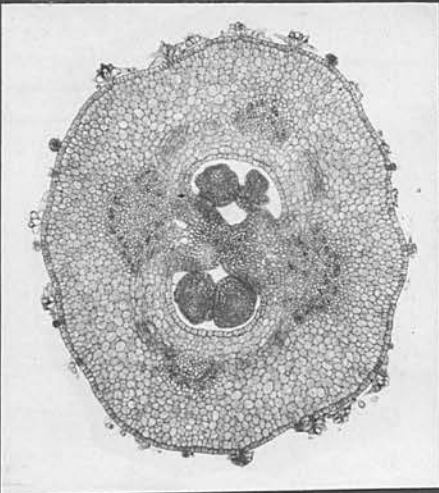


Fig. 11

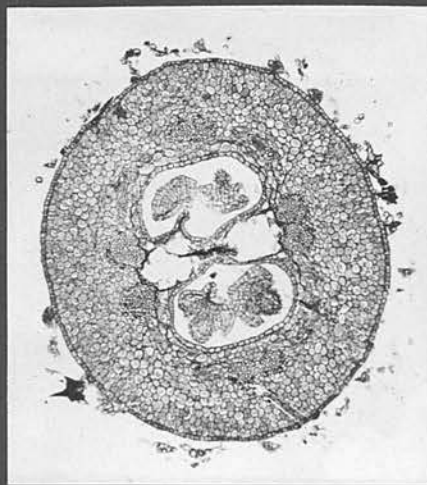


Fig. 12

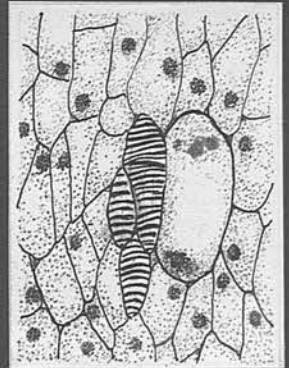


Fig. 13

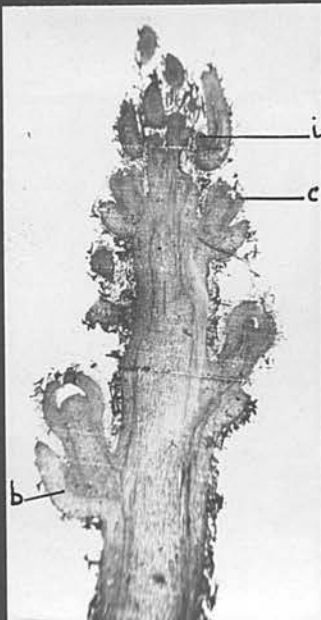


Fig. 14

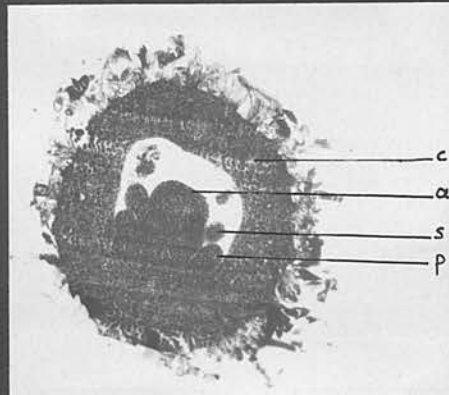


Fig. 15

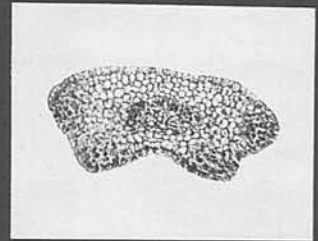


Fig. 16

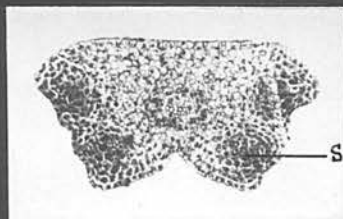


Fig. 17

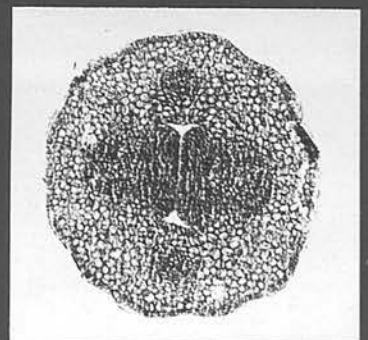


Fig. 18

Fig. 19 Calyx hairs, surface view, from unstained
preparation. X 45.

Fig. 20 Hairs viewed from above X 150.

From unstained preparation.

(a) leaf hair

(b) calyx "

(c) petal "

(d) petiole "

Fig. 21 Hairs on ovary. X 300.

From stained section of ovary.

(a), (b) peltate hairs

(c) sessile hair.

Fig. 22 Hairs on leaf. X 300.

From stained section of leaf. Compare with
Fig. 21.

(a), (b) peltate hairs

(c) sessile hair.



Fig. 19

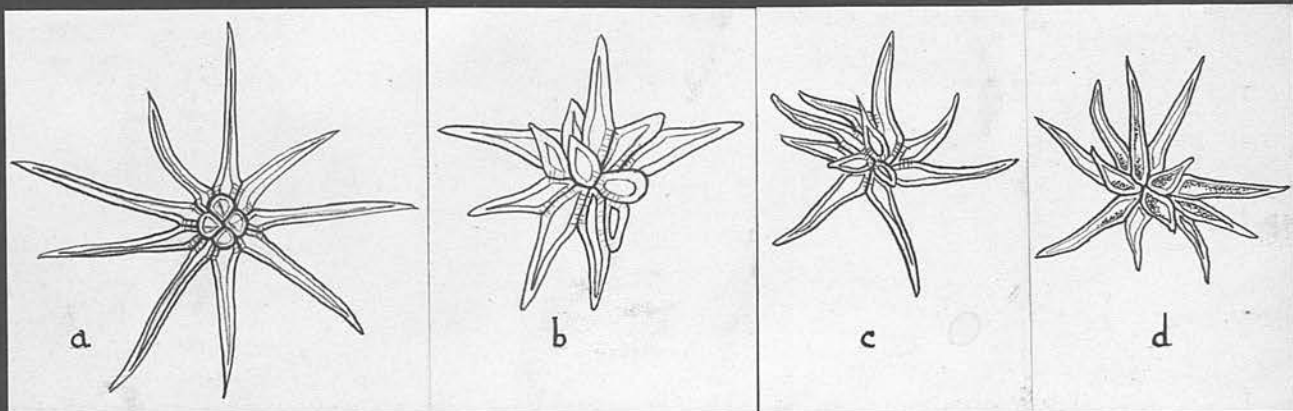


Fig. 20

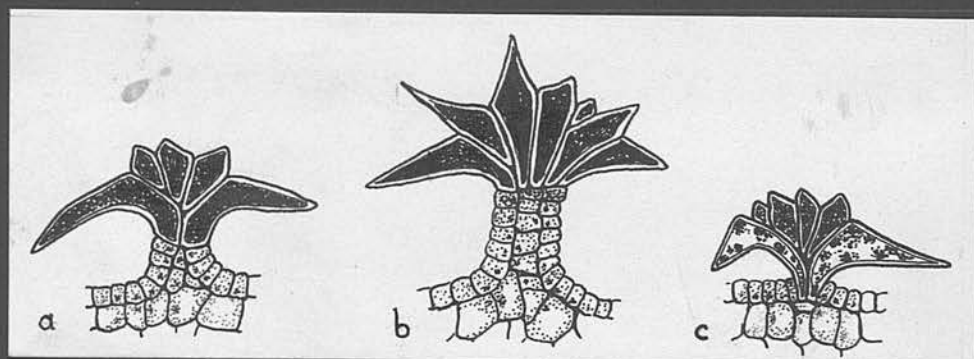


Fig. 21

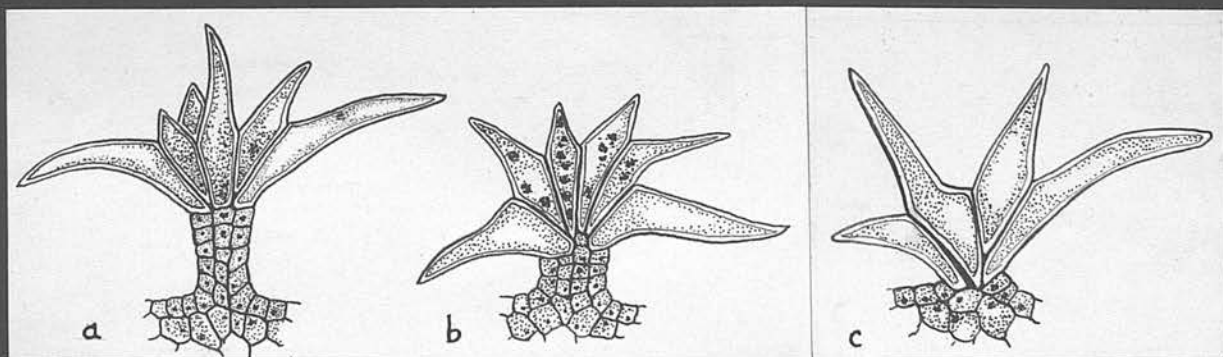


Fig. 22

Fig. 23 Upper epidermis of leaf. Surface view X 500.

Fig. 24 Lower epidermis of leaf. Surface view. X 500.

Fig. 25 Leaf palisade. Horizontal section X 500.
 showing secretory cells.

Fig. 26 Leaf mesophyll. Horizontal section X 500.
 showing secretory cell.

Fig. 27 Leaf lamina. T.S. X 450.
 showing secretory cell and two lateral veins.

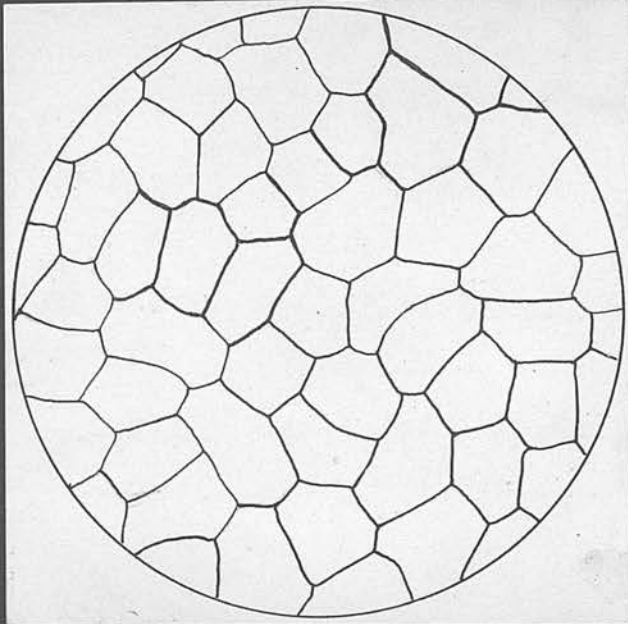


Fig. 23

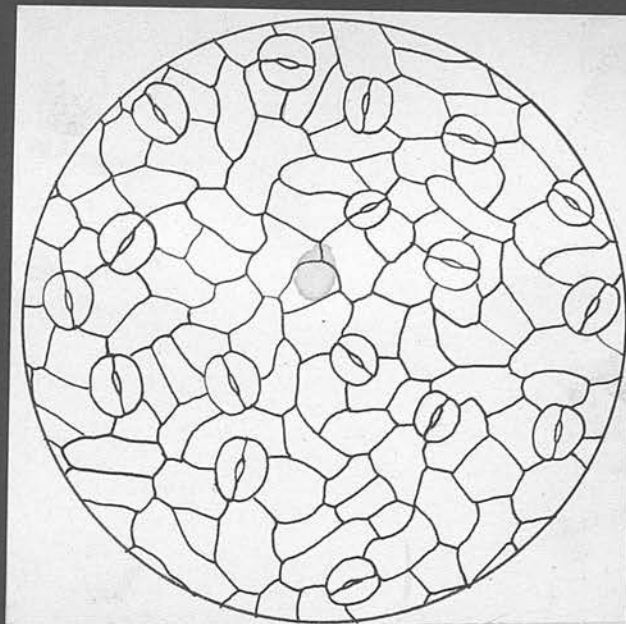


Fig. 24

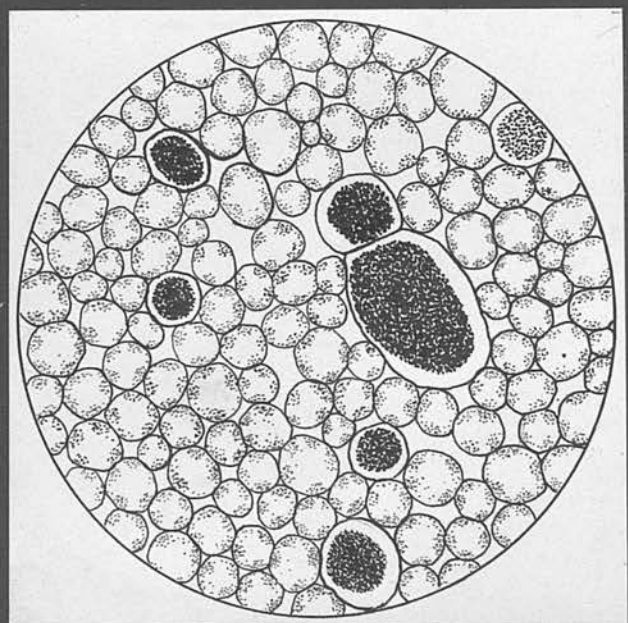


Fig. 25

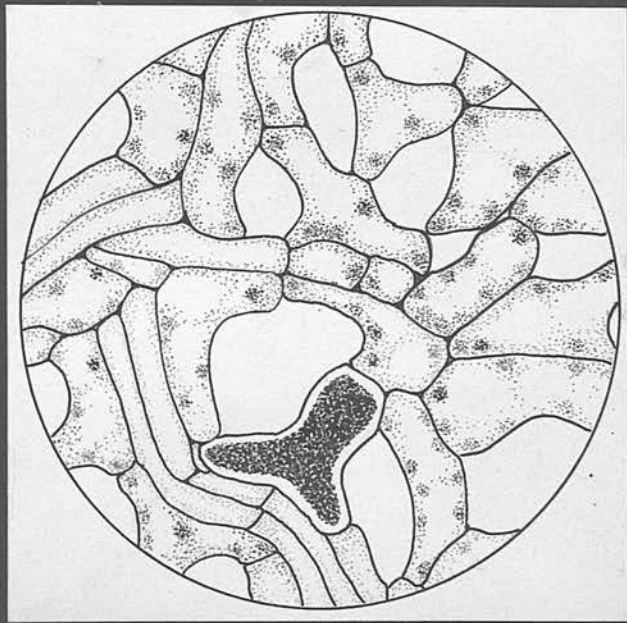


Fig. 26

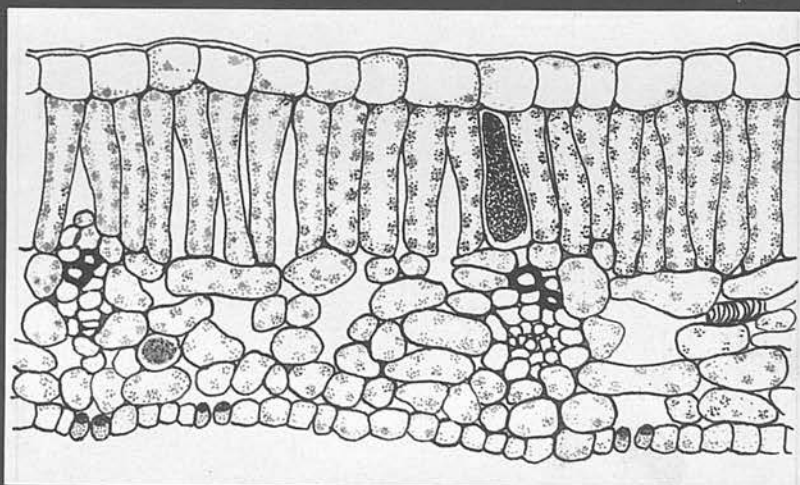


Fig. 27

Fig. 28 Petiole vascular strand. T.S. X 50.
from centre of petiole.

Fig. 29 Marginal meristem of leaf initial. T.S. X 25.
h hair initial

Fig. 30 Young leaf lamina. T.S. X 450.
The upper hypodermal layer is differentiating
into palisade.

Fig. 31 Leaf bud. T.S. X 25.

Fig. 32 Young leaf. T.S. X 45.

Fig. 33 Stem apex. L.S. X 35.
l leaf initial

Fig. 34 Stem apex. L.S. X 300.
Detail of fig. 33.

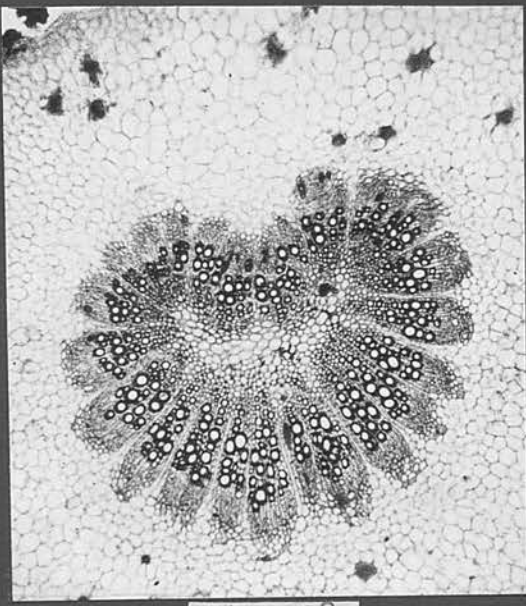


Fig. 28

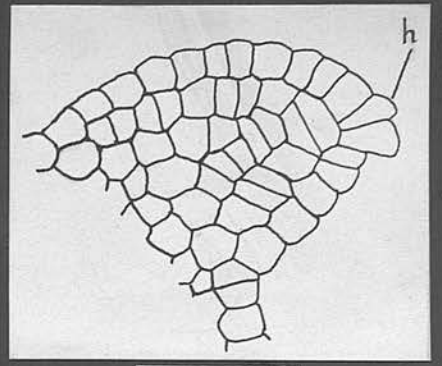


Fig. 29

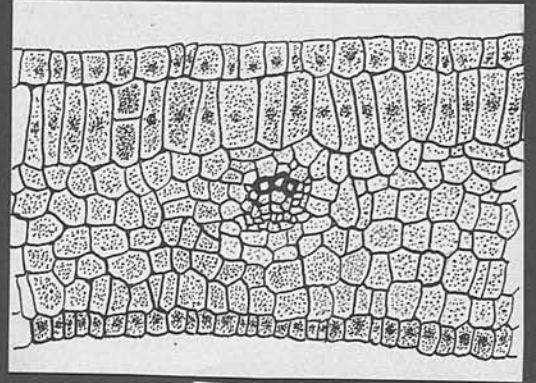


Fig. 30.



Fig. 32

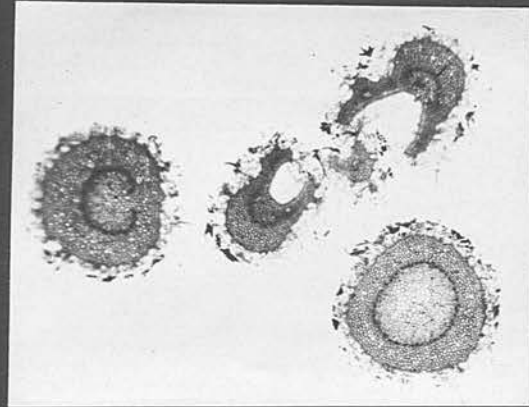


Fig. 31



Fig. 33.

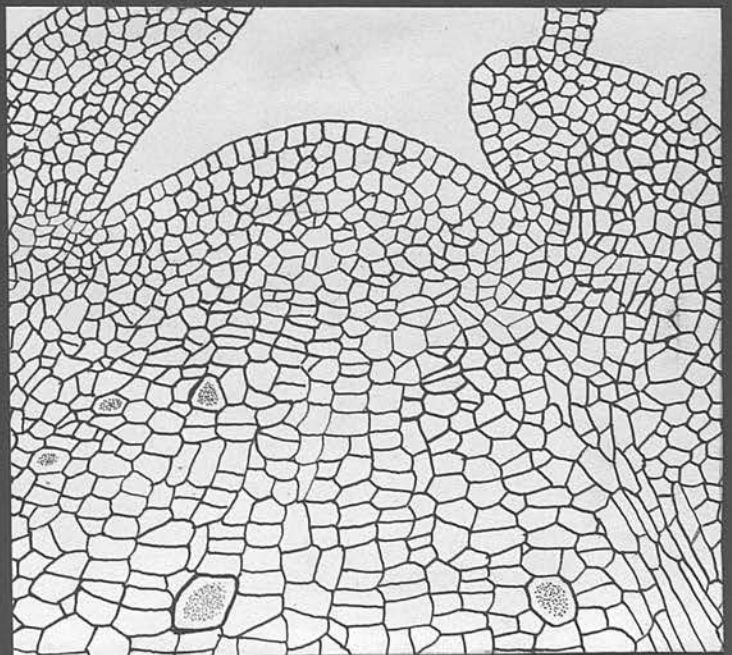


Fig. 34.

Fig. 35 Pericyclic fibres. T.S. X 350.

Fig. 36 Stem. T.S. X 30
 showing one year's secondary growth.
 f pericyclic fibres

Fig. 37 Secondary phloem. T.S. X 50.
 Showing dark tangential bands of bast fibres.

Fig. 38 Secondary xylem. T.S. X 100.
 The lightly stained rings are due to xylem
 parenchyma.

Fig. 39 Secondary xylem. T.S. X 300.

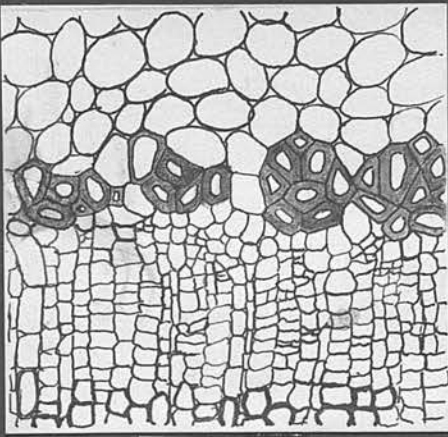


Fig. 35

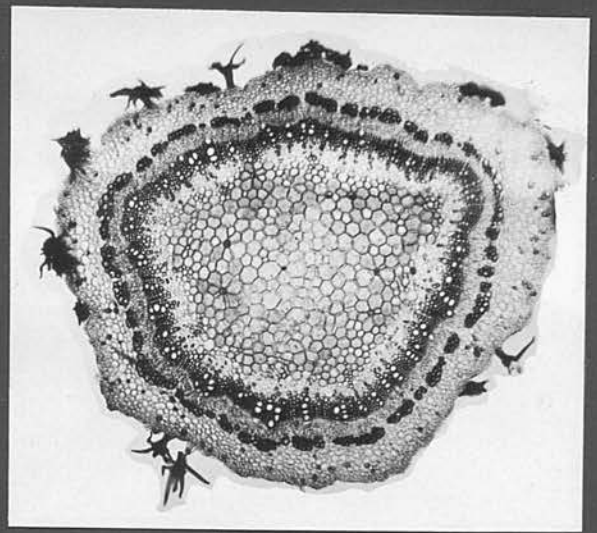


Fig. 36

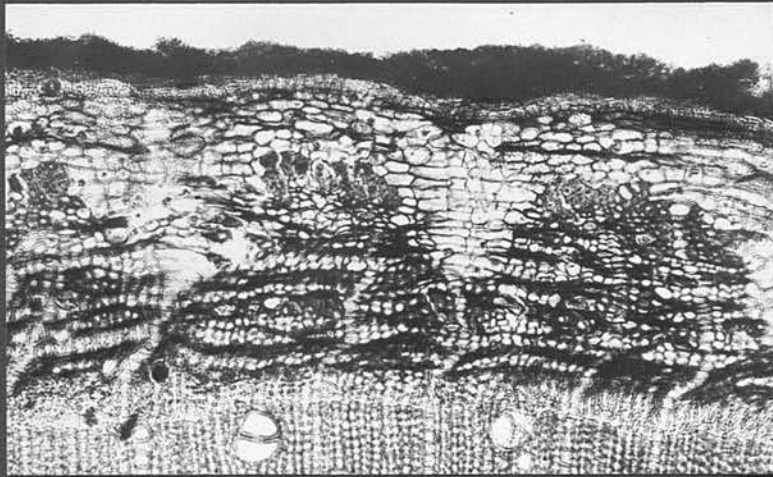


Fig. 37

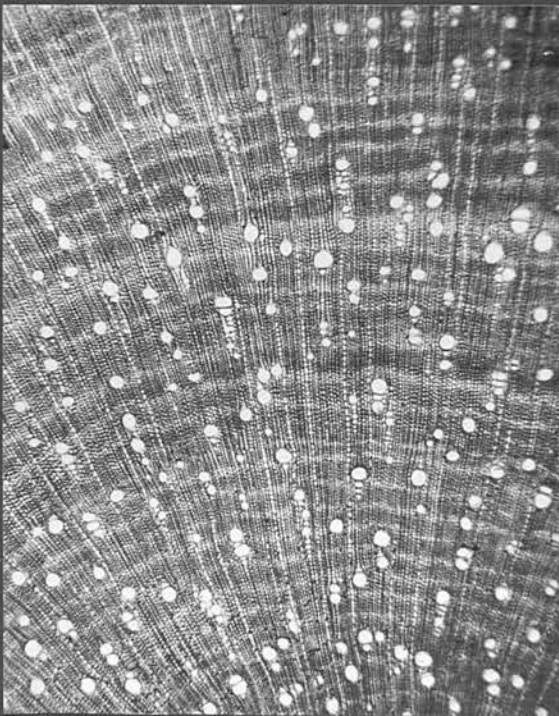


Fig. 38

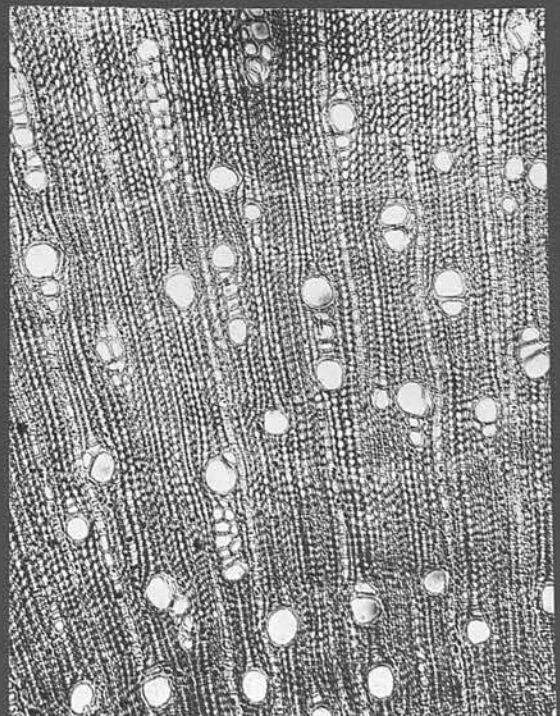


Fig. 39

Fig. 40 Secondary xylem. L.T.S. X 50.
showing short vessel segments and starch
granules in the wood parenchyma.

Fig. 41 Secondary xylem. L.T.S. X 100.

Fig. 42 Secondary xylem of root. T.S. X 35.

Fig. 43 Secondary xylem of root. L.T.S. X 100.

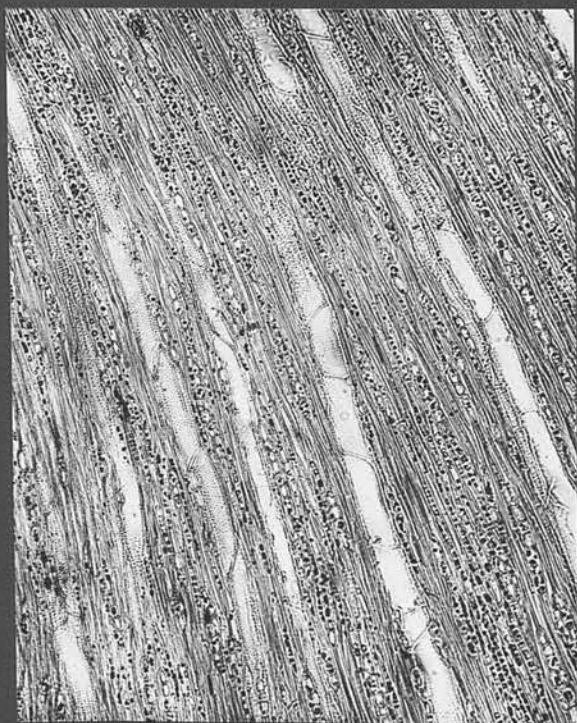


Fig. 40

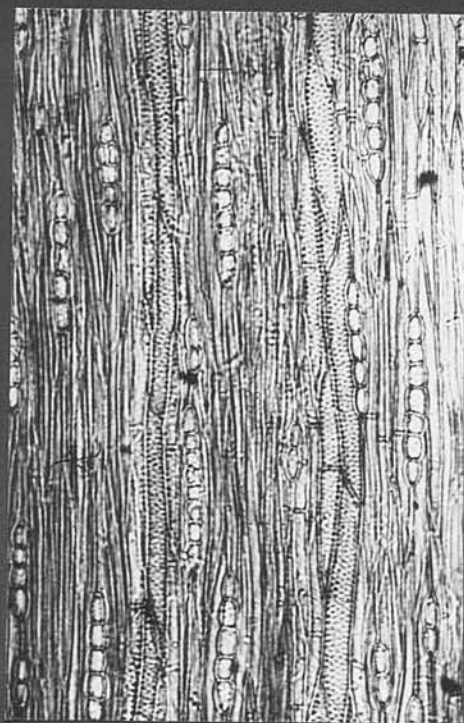


Fig. 41

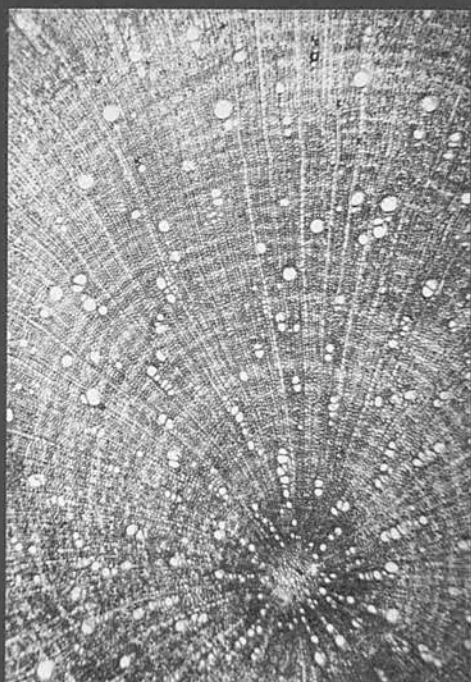


Fig. 42

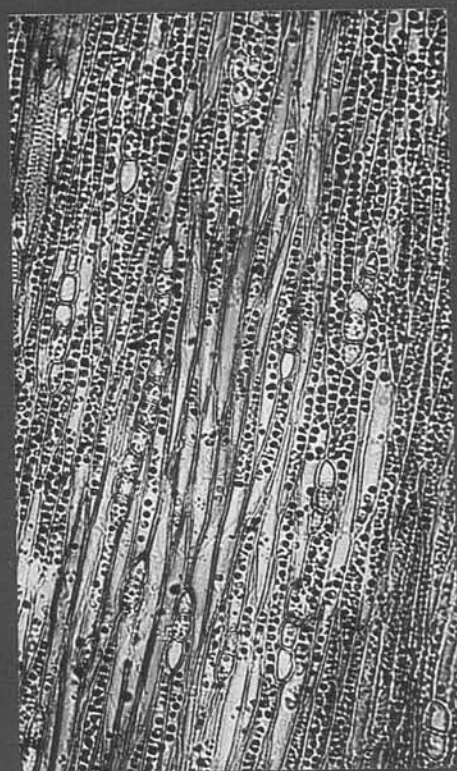


Fig. 43

THE GENUS VALLEA MUTIS.

The genus *Vallea* is endemic in South America and its natural distribution in the sub-continent is restricted to the eastern and western slopes of the Andean mountain range. *Vallea* is unusual among Tiliaceous genera in South America in inhabiting only cold or cold temperate regions; other genera of Tiliaceae, such as *Prockia*, *Corchorus*, *Muntingia* and *Truimfettia*, are warm temperate or sub-tropical in their distributions; others, including *Apeiba*, *Luhea* and *Sloanea* are found only in temperate regions.

The species *Vallea stipularis* Linn. f. (Fig. 1) occurs at altitudes of between 2,000 and 3,800 metres from Venezuela through Columbia and Ecuador to Peru, Bolivia and northern Argentina, a longitudinal range of about 2,500 miles. It forms, according to Rimbach (1932), one of the characteristic trees of the highest forests of Ecuador which extend up the mountain slopes as far as 3,400 metres which is the general limit of tree growth, though single trees may reach 4,000 metres in sheltered situations. It is known to occur "in hedges and scrub around Bogota (Columbia) and in gardens of old villas outside the town" (Ballard (1934)).

Vallea stipularis in its native habitat is a small tree with purplish-brown bark and slender glabrous branchlets bearing alternate dark-green leaves and cymes of rose-coloured flowers. It may attain a height

of 10 metres and a stem diameter of 30 cms., according to Record and Hess (1943).

Taxonomic history of the genus *Vallea* Mutis.

Vallea stipularis was discovered in Columbia (then known as 'New Granada') by Joseph Celestin Mutis, a Spanish doctor, in the middle of the 18th Century. Mutis founded the genus, naming it in memory of the botanist Felix Vallei, whose 'Florulae Corsicae' was published in 1762.

The genus and only species *Vallea stipularis* were described by the younger Linnaeus in the 'Supplementum Plantarum' of 1781. An illustration of the plant cited in the specific diagnosis is included in a large unpublished collection of drawings by Mutis which is now in the herbarium of the Botanic Garden at Madrid.

The classical generic description of the genus *Vallea* in the 'Supplementum' of 1781 was given under the 'Polyandria Monogynia' group of the Linnean system. Antonii de Jussieu (1789) in his 'Genera Plantarum' relegated it to his "genera of doubtful affinity" though he established a group 'Tiliaceae'.

The genus was first assigned to a definite family by De Candolle (1824) who placed it in his Order Elaeocarpaceae which he separated from the Tiliaceae on the grounds of the floral characters of divided petals and linear anthers dehiscing by apical pores.

Endlicher (1836) included *Vallea* within the Tiliaceae in the second sub-order Elaeocarpeae which

he differentiated from the remainder of the family (the 'Tiliaceae verae') by the same floral characters (lobbing of petals, apical dehiscence of anthers) as had previously been used by De Candolle to separate the Elaeocarpaceae as a distinct Order.

Bentham and Hooker (1862) retained the Elaeocarpeae within the Tiliaceae. With Endlicher's Tribe Sloanieae and the newly founded Prockieae it became the series Heteropetalae, distinguished from the remainder of the family (Holopetalae) by its "absent, sepaloid or divided, rarely truly petaloid, petals, valvate or variously imbricate but never contorted in the bud". Vallea was placed in the Tribe Sloanieae distinguished from the Tribe Elaeocarpeae by the position of insertion of the perianth.

No new arrangement of the Tiliaceae of any importance was made until 1895 when Engler and Prantl published their 'Naturliche Pflanzenfamilien'. In this system the Heteropetalae of Bentham and Hooker (with the exception of the Tribe Prockieae) were again removed from the Tiliaceae and placed before it as the family Elaeocarpaceae, chiefly on account of negative anatomical characters such as the absence of mucous elements but little detail is given. Floral characteristics used to distinguish the Elaeocarpaceae are the often divided petals, never convolute in the bud, and the free stamens dehiscing by apical pores or slits. Vallea is placed in the Tribe Aristoteliaceae distinguished from the Tribe

Elaeocarpeae by its always free, imbricate petals and "flat disc". The Tribe Elaeocarpeae has free or united petals and a "cushion-like disc".

Hutchison (1926) reverted to the system of Bentham and Hooker by re-incorporating the Elaeocarpaceae within the Tiliaceae. Edlin (1935) suggested a similar revision of their position, placing them as the Tribe Elaeocarpeae and Aristoteliaceae (as constituted by Engler and Prantl) before the remainder of the Tiliaceae.

The genus *Vallea* differs from the more typical genera of Tiliaceae by several anatomical features which naturally separate it, together with six or seven allied genera, as a distinct sub-section from the remainder of the family. Some authorities have favoured the removal of this group from the Tiliaceae proper and its raising to the status of a separate family. Evidence for this view will be considered at the end of this paper.

Synonymy.

The original description of the species *Vallea stipularis* by the younger Linnaeus in the 'Supplementum Plantarum' of 1781 is very brief, hence it is difficult to judge whether similar plants described by later authors are synonymous with the Linnaean plant.

Since the original description of *Vallea stipularis* was published eight additional species of *Vallea* have been described, based mainly on differences in the

degree of pubescence and the shape of the leaves and stipules. These characters are very variable, especially the leaf shape (extreme variations of which are often found in individual plants) resulting in a certain amount of confusion, some of the described 'species' being probably mere varieties of a variable species-type.

The chief points in the Linnaean description of *Vallea stipularis* are as follows: "Leaves alternate, stalked, cordate, entire, hairy below. Petioles shorter than the lamina. Stipules sessile, reniform, amplexicaul, entire, rather large. Panicle branched, terminal." No mention is made by Linnaeus of pubescence on the stem or of its distribution on the lower surface of the leaf. Presumably the stem was glabrous as pubescence on the leaf was specially noted.

In later descriptions glabriety of the branchlets was taken as a constant feature of *V. stipularis* L.f. Linnaeus noted that the floral parts varied from 4 to 5.

The plants used in the present investigation agree with Linnaeus' description except that the leaves vary in shape from cordate to broadly-ovate and the stipules are rather small. Pubescence is confined to the basil axils of the midrib and lateral veins on the lower surface of the leaf. A varietal name based on a species published by Turczaninoff (1858) was proposed for this form by Ballard in the Botanical Magazine 1934. ("*Vallea stipularis* var. *pyrifolia* F. Ballard var. nov.")

(1) The "*Vallea stipularis*" of Humbolt, Bonplard and

Kunth (1821) differs from the *V. Stipularis* of the 'Supplementum' only in the restriction of the pubescence on the leaf to the lower axils of the veins and in the possession of stalked stipules. Since Linnaeus gave no information regarding the distribution of hairs on the leaf, apart from the fact that they occurred on the lower surface, it is impossible to say whether the leaves of Kunth's plant were exactly similar to those of Linnaeus'. The stipules of *V. Stipularis* HBK were evidently only very shortly stalked as they are described as being much shorter than the petioles, so that it is possible that this plant is synonymous with *V. stipularis* Linn.f.

(2) The "*Vallea stipularis*" recorded by De Candolle (1824) is undoubtedly the same plant as *V. stipularis* HBK. The leaves were "obtusely cordate, roughly hairy beneath the vein axils and at the base", the stipules were reniform and shorter than the petioles.

(3) "*V. Stipularis* Linn.fils" is recorded by Triana and Planchon (1862) in their Flora of New Granada (now Columbia) as occurring between 2,000 and 3,000 metres in the Andes of Bogota. No description of the plant is given. Synonyms given are *V. cordifolia* Ruiz et Pavon, *V. ovata* Turcz. and *V. pyriformis* Turcz.

(4) "*Vallea cordifolia* Ruiz et Pav.," recorded from Peru by Ruiz and Pavon (1798) in their Flora of Peru and Chile is probably not synonymous with *C. stipularis* L.f. No mention of any pubescence is made in the very.

brief description ("leaves cordate, acute; stipules reniform, stalked") but later authors (DC., Miers) describe a species under this name as having tomentose twigs, petioles and pedicels and leaves which are hairy below chiefly on the nerves and at the base.

(5) "V. glabra Miers" (1860) Its author describes this as a distinct species approaching *V. cordifolia* in its lack of stipules. His specimens had glabrous branchlets; truncate, non-cordate, ovate leaves, pale-green above (unusual in *Vallea* the leaves of which are generally dark-green above), glabrous "unless the axils of the nerves are hairy" (he seems uncertain of this feature) and glabrous, "evidently exstipulate" petioles.

Stipules are an inconstant feature of *Vallea* and it is quite possible that on the specimen described by Miers they were absent. Because of their absence and the complete lack of hairiness (though this is doubtful) he considered this plant to be a separate species distinct from *V. Stipularis* L.f. which he states was "very well figured and described by Kunth". It is probable that his description was based on an atypical or imperfect specimen of *V. Stipularis* L.f.

(6) "Vallea pyrifolia Turcz." Recorded from the Andes of Quito (Ecuador) at 9,000 - 12,000 feet by Turczaninoff in 1858. This plant was glabrous except for hairiness in the lower axils of the veins of the leaf, in which respect it resembled the *V. stipularis* of Humbolt, Bonplard and Kunth. The stipules,

however, were "nearly all deciduous, only the upper ones shortly stalked" and rhomboid. Reniform, not rhomboid, stipules are present in *V. stipularis* L.f. and this character, if constant, would seem to distinguish *V. pyrifolia* Turcz. from the Linnaean species.

(7) "*V. Schlimii* Turcz." (1863) recorded from the Sierra Nevada (Venezuela) at 11,000 feet. This plant had leaves similar to those of *V. Stipularis* L.f. but smaller and "densely hairy in nerve axils". Stipules are not mentioned in Turczaninoff's description. The flowers were half the size of those of *V. stipularis*, deep red, and, a curious feature, the petals were shorter than the calyx 'petala calyce breviora'. This feature makes Turczaninoff's plant distinct from *V. stipularis* L.f. in which the petals are nearly twice the length of the sepals.

Uses and Cultivation.

Vallea does not furnish any products of commercial importance. The wood is hard, reddish-brown in colour, of fine grain and compact texture similar to that of Birch, and is suitable for use as a veneer in cabinet making, but the small size and limited occurrence of the trees would make commercial exploitation unprofitable.

The leaves of *V. cordifolia* Ruiz et Pav. yield a yellow dye. Though not synonymous with *V. Stipularis* Linn.f. this plant is very similar.

The flowers have decorative qualities but the plant is still a horticultural novelty in this country.

It will flower outside in spring in the South of England if protected from frost during the winter, and is suitable for training against sheltered walls.

Material.

The material used in this investigation was obtained from two plants of *Vallea stipularis* growing in the glasshouses at the Royal Botanic Garden, Edinburgh. The first plant is a small shrub growing in the Alpine House; it is kept pruned to a height of about 3 feet and flowers regularly in May. It was obtained from Wisley in 1937. The second plant is trained on wires against the wall of the main corridor of the Temperate House and as yet has not flowered. It was obtained as a cutting from plants at Kew which were raised from cuttings brought from the Colombian Andes by Mrs Tracey.

Young root-tips were obtained from a cutting, struck in the gardens.

Methods.

For methods of fixation, sectioning and staining of material see previous paper on *Steriphoma*.

VALLEA STIPULARIS L.f. VAR. PYRIFOLIA F. BALLARD

A large shrub or small tree, up to 4.5 m. or rarely 6 m. high. Branchlets slender, glabrous, becoming woody with a smooth longitudinally-striated purplish-brown bark.

Leaves deciduous, very variable in size and shape, ranging from lanceolate to broad-ovate or sometimes almost palmatilobed, rounded or deeply cordate at the base, acute or slightly obtuse; 2.5-5cm. long, 1.5 - 4 cm. broad; rather leathery; dark green above, paler glaucous-green below, often tinged with purplish-red especially during Autumn; glabrous except for small tufts of brown hairs in the basal axils of the midrib and lateral veins on the lower surface. Petioles slender, glabrous, terete, pale-green; half as long as the lamina or slightly longer. Stipules broadly reniform, amplexicaul, green and leafy, very shortly stalked or sessile; larger on vegetative shoots, up to 1.5 cm. broad and 1 cm. long.

Inflorescence lateral or terminal, cymose, leafy, peduncles and pedicels glabrous, pedicels swollen immediately below flower; 2 or 3 flowers to a peduncle. Bracts when present small and green. Bracteoles sometimes present at junction of peduncle and pedicel, paired, very small, green. Flowers 1 cm. across. Sepals 3-5, commonly 4; free, valvate in the bud; pale rose in colour, paler on the inside with darker veins; glabrous except for short white hairs along

margin and at apex; oblong lanceolate, acute; 3-4 mm. wide, 5-6 mm. long. Corolla open, cup-shaped, Petals 3-5, commonly 4 as sepals; imbricate; deep rose in colour, obovate in profile; 8-10 mm. long, 6-8 mm. broad; trilobed for nearly half their length; glabrous, smooth; lobes suborbicular to ovate-oblong, the middle one on the outside and overlapping the other two.

Hypogynous disc fleshy, crenulate, shiny, consisting of 2 annular ridges between which the stamens arise in depressions. Stamens 25-35, in 2 series; filaments rose-coloured, broad at base and tapering upward, curving inwards and upwards against ovary; densely tomentose, especially at base, with long white hairs; 3 mm. long when straightened out; anthers 2-3 mm. long, olive brown, white tomentose, quadrilocular, introrse, dehiscing by 2 oblique pores at apex. Ovary ovoid, dark-green, glabrous, shiny, with 3-5 longitudinal furrows according to number of carpels; Carpels 3-5, commonly 4, fused; loculi 3-5 with 2 ovules in each loculus; style 5-7 mm. long, slender, glabrous, rose-coloured, dividing into 3-5 filiform stigmas which are often uneven in length and about one-third the length of style.

Fruit a small globose capsule, covered with fleshy tubercles, dehiscing imperfectly at the apex into 3-5 valves. Seeds scarlet, with aril.

The Flower.

The symmetry of the floral parts of *Vallea* varies from 3 to 5. Linneaus noted in 1781 that it could

vary from 4 to 5. The flowers of the plants at Edinburgh are most commonly tetramerous, occasionally pentamerous, and rarely trimerous.

Floral formula: K 3-5, C 3-5, A 25-35, G (3-5)

The Perianth. The valvate aestivation of the sepals and the imbrication of the petals can be seen in Fig. 5. The petals usually overlap each other but occasionally in pentamerous flowers the anterior petal overlaps the outside of the two petals adjacent to it.

The Androecium. The number of stamens is not necessarily a multiple of the numerical symmetry of the other floral whorls. Trimerous flowers have been observed with 25 and 27, tetramerous flowers with 26, 30, 31, 32 and 33, and pentamerous flowers with 33 and 35 stamens.

Each bilocular anther dehisces by an oblique apical pore as shown in Fig. 7. The attachment of the anthers to the filaments is basal. The curvature of the filaments can be seen in Fig. 2.

The hairs on anthers and filaments are simple, non-septate extensions of epidermal cells, shorter and less dense on the anthers than on the filaments. A simple epidermal hair on an anther-lobe is well shown in Fig. 10.

The yellow pollen is abundantly produced. The individual grains are small (from 8 to 10 in diameter),

rotund, and hyaline.

A curious feature of the flower is the situation of the carpels opposite the petals (see Fig. 3.). This would be expected if there was only one whorl of stamens to alternate with the carpels and petals or if there were 3 whorls, but the stamens are actually inserted around the ovary in 2 series. The double whorl of stamens must therefore be due to either (a) the splitting of a former single whorl of stamens or (b) the suppression of the outer of a former 3 whorls of stamens. There is no vascular trace of a third staminal ring.

The Ovary. Ovule placentation at the base of the ovary is axile, the 2 ovules in each loculus being attached to the centre of the axial column formed by the fused edges of the carpels. The ovules are superposed one above the other; the upper ovule is erect in the loculus, the lower is pendulous. This arrangement of the ovules is shown in Fig. 14.

Central fusion of the carpel margins becomes less complete near the centre of the ovary so that the ovules become practically parietal in their placentation, as seen in Fig. 12. The margins of the carpels fuse imperfectly at the apex of the ovary (Fig. 13) and up the length of the style, ultimately separating completely when the latter splits into 3 to 5 stigmatic lobes according to the number of carpels.

Abortion of one of the two ovules in each loculus

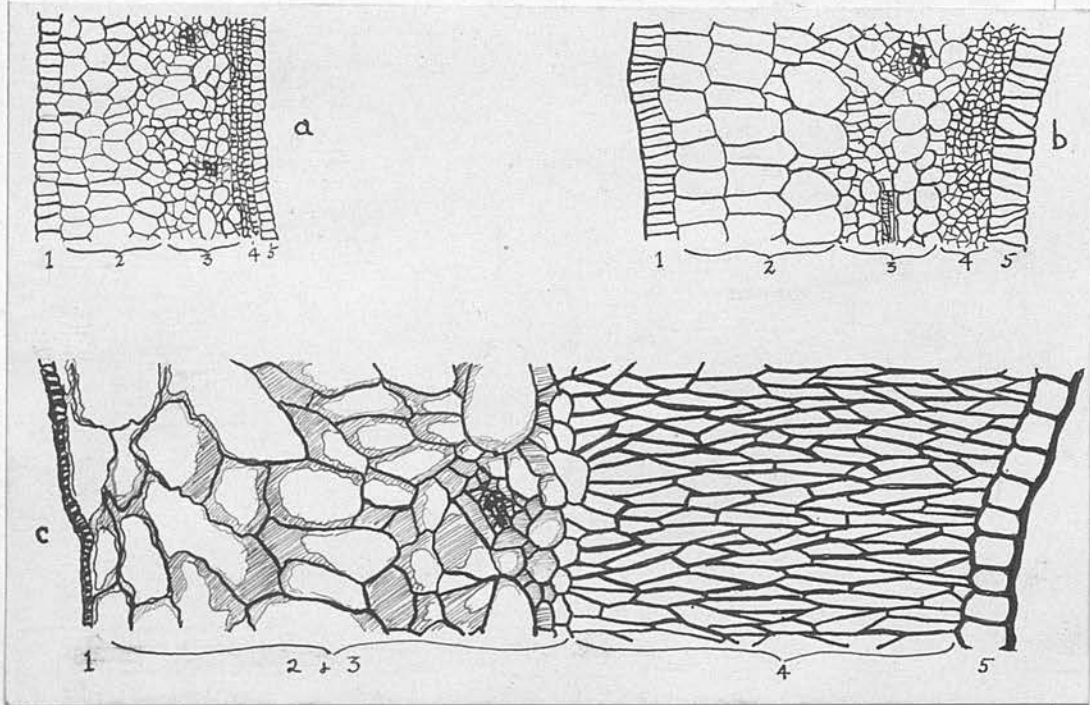
is frequent in the plants used in this work. *Vallea stipularis*, however, rarely sets seed in this country and ovule abortion may be the first sign of degeneration in the ovary.

The ovules are of the normal anatropous type with double integument.

Fruit and Seed.

Though the majority of the ovaries matured on the plant at Edinburgh the seeds inside were small and shrivelled. The fruits reached a maximum size of 1 cm. diameter and dehisced irregularly at the apex into as many valves as the number of carpels. The inner surface of the pericarp thus exposed was crimson in colour, the outer surface being green and covered with fleshy protruberances. Most authors describe the fruit of *Vallea* as capsular, though Ballard (1934) describes it as a globose berry, and Miers (1860) states "the fruit is baccate, the mesocarp thick and fleshy and covered by a thin epicarp which is corrugated in the form of many fleshy obtuse tubercles; this dries upon the testaceous endocarp after the fall of the fruit, which becomes imperfectly dehiscent at its summit". As the fruit dehisces, though but imperfectly, it is more correctly described as capsular than baccate.

A few ripened seeds were obtained. They were bright red in colour and about 4 mm. in length including a small aril.

Development of fruit and seed.

Text - Fig. 1. Development of fruit wall x 120.

The ovary wall, before fertilization, occurs, shows 5 types of tissue (Text - Fig. 1a) - (1) an outer epidermal layer of small cells, (2) several palisade-like layers of slightly elongated cells, (3) numerous layers of cells varying in size, some being very large, (the vascular bundles traverse this layer), (4) several closely-packed layers of small cells with large nuclei; (5) the inner epidermis lining ovarian cavities.

During maturation the ovary wall increases greatly in thickness, the tissues becoming much altered in appearance and relative thickness, and there is a general increase in cell size. Cell division occurs in the fourth layer next to the inner epidermis (1b 4)

and great radial elongation of the resulting cells causes it to occupy half the thickness of the ripe fruit wall (1c 4). The cell walls become thickened and lignified so that this layer could be termed a "stony layer" or endocarp. Cell division also occurs at certain points in the "palisade" and third layers, forming fleshy tubercles on the outside of the fruit (Fig. 15). Enlargement and loss of contents takes place generally (1c); there is no great development of the vascular bundles.

Development of the seed could not be followed because of the scarcity of maturing seeds. The straight, dicotyledonous embryo of the ripe seed is surrounded by abundant endosperm containing numerous starch grains (Fig. 16). The testa is very hard due to two innermost layers of stone cells with greatly thickened walls and very small cavities.

The Leaf.

The dorsiventral lamina has pinnate venation. Hairs occur only on the lower surface, in the basal axils of the midrib and lateral veins. Each hair is simply a long tapering extension (up to 1 mm.) of an epidermal cell and is generally unicellular though occasionally sparsely septate. Hairs were found to be most abundant on the leaves of fertile shoots.

The leaf shows no unusual anatomical features except an extraordinary papillation of the lower epidermis. Stomata are present only on the lower

surface. The lamina varies only slightly in thickness from 140 to 200 μ .

The upper surface is smooth and is covered with a thin cuticle. The upper epidermis (Fig. 17) consists of a single layer of large colourless cells which are irregularly pentagonal or hexagonal in surface outline, 15-20 μ in breadth, 15 μ in depth, and slightly elongated above the veins and midrib.

Palisade tissue, containing numerous chloroplasts, lies immediately under the upper epidermis and occupies slightly less than half the thickness of the lamina.

Spongy mesophyll tissue occupies the remaining thickness of the leaf and consists of large rounded cells with fewer chloroplasts and many inter-cellular spaces.

The lower epidermis (Fig. 18) consists of a single layer of cells which are slightly smaller than those of the upper epidermis. Except above the midrib, each cell is drawn out into a broad obtuse papilla about one and a half times the depth of the base of the cell (Fig. 19). Because of this feature it was found impossible to obtain satisfactory surface preparations or collodion casts of the lower epidermis.

(No mention of this remarkable feature is made in the literature concerning *Vallea* but the detailed anatomy of this genus has not previously been investigated. *Vallea* appears to be unique among the Heteropetalous Tiliaceae in the possession of a

papillate lower epidermis).

Stomata occur on the lower leaf surface only and are irregularly distributed in patches between the veins. They are not orientated in any definite way with regard to the veins or midrib. The stomata are difficult to see in surface view because of the projecting epidermal papillae but they may be distinguished by a surrounding ring of very slightly elongated epidermal cells. Each stoma consists of a pair of curved guard-cells situated level with the base of the epidermal cells. The guard-cells vary in size (from $20-25\mu$ in length, $8-10\mu$ in breadth) and possess the usual large nucleus and chloroplasts.

There are no special subsidiary cells and the stoma pore does not lead into any definite sub-stomatal cavity in the mesophyll.

Small rhomboidal crystals of Calcium oxalate are occasionally found scattered throughout the palisade tissue.

The vascular system of the lamina consists of a midrib and 4 to 7 alternate main lateral veins linked by a network of finer veins. The midrib projects prominently from the lower surface of the lamina, and the lateral vein slightly.

The vascular tissue of the midrib is in the form of 8 to 12 small xylem-phloem bundles closely arranged to form an open arc with more or less incurved ends (Fig. 20). There is no sclerenchymatous sheath.

Immediately below the arc of vascular tissue lie two or three layers of small parenchymatous cells; surrounding these and the vascular strand are several layers of larger, closely-packed parenchymatous cells which, below the vascular strand, form a mass of tissue becoming sclerenchymatous near the lower epidermis. This mass of tissue projects from the lower surface of the lamina. Above the vascular strand is small-celled, slightly sclerenchymatous tissue.

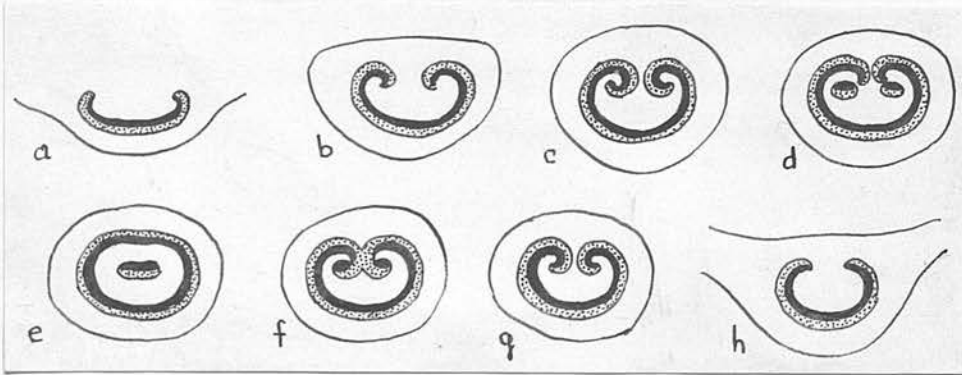
The lateral veins consist simply of a collateral vascular strand surrounded by a sheath of large, empty, cells extending to both the upper and the lower epidermis.

The petiole. The cortex consists of two zones - an outer of small sclerenchymatous cells and an inner of larger parenchymatous cells. Several layers of parenchymatous cells surround the stele and penetrate between the groups of phloem.

Small rhomboidal crystals of calcium oxalate similar to those found in the lamina and stem are scattered singly throughout the parenchymatous inner cortex and medulla. They are clearly visible in Fig. 22. Small spherical or ovoid starch bodies are numerous in medulla, xylem and cortex, staining dark blue in dilute iodine solution.

The vascular system of the petiole consists mainly of 20 to 30 small xylem-phloem bundles closely placed together to form, for the greater part of its length, a closed cylinder of vascular tissue which

opens out into an arc at the base of the petiole and on entering the midrib.



Text - Fig. 2. Vascular system of petiole. Diagram

The leaf trace (Text Fig. 2a) comes off from the main stele as a slightly curved collateral strand of xylem and phloem which passes out through the cortex of the stem into the base of the petiole. The ends of this vascular strand gradually curve upwards and inwards (2b, c) and eventually separate off into two small collateral medullary bundles which fuse into one (2d, e). At this point the remainder of the vascular tissue forms a completely closed cylinder and remains so for the greater part of the length of the petiole. On nearing the lamina the reverse process occurs - the medullary bundle splits into two, the closed cylinder of vascular tissue opens and the two small medullary bundles fuse with the ends of the arc of vascular tissue. (2f, g, h). Before fusion they may persist for a short distance of the midrib.

The Stem.

The young stem remains in the primary condition for only a very short while. Secondary growth begins

early even in rapidly-elongating vegetative shoots.

The epidermis in young stems, before secondary growth has been active enough to rupture it, consists of a single layer of small cells, covered by a thin cuticle. The cortex underlying the epidermis is rather narrow, and is differentiated into two zones: an outer zone of rather small, closely-packed, thicker-walled, lignified cells, and an inner zone of larger, thin walled, more loosely-packed cells. (see Fig. 22).

Small groups of lignified pericyclic fibres begin to form internal to the cortex in the young stem and are well-developed before secondary growth begins in fertile shoots. In quick-growing vegetative shoots they are formed later. The groups of fibres are closely placed forming, in transverse section, a but slightly interrupted ring as seen in Fig. 33. In longitudinal section they are seen to anastomose and divide, forming a cylindrical network of mechanical strengthening tissue internal to the cortex. The young fibre cells possess cavities with living contents (Fig. 22); the increasing thickness of the walls obliterates the cavity in older fibres (Fig. 24). Stratification of the walls is visible in transverse sections. The individual fibre elements have a small diameter of $6-10\mu$ but are comparatively very long, some attaining a length of 6 m.m.

Internal to the cortex and fibrous pericyclic ring lie the vascular tissue and pith.

The vascular tissue is never disposed in distinct

bundles sharply separated by parenchymatous medullary rays, but in the very young primary stem 20 to 30 small groups of protoxylem elements can be distinguished around the central pith, each with cambial tissue and a small area of phloem tissue external to it. The protoxylem elements have walls which are spirally or annularly thickened.

The wide pith is composed of large, thin walled parenchymatous cells, a number of which are smaller and more rounded than the cells surrounding them. It was thought that these might be tannin-containing elements similar to those found in related genera but testing of fresh material with ferric chloride solution gave negative^{results}, and stained sections did not show any differentiation between these cells and the remainder of the pith. (See Fig. 23).

The pith cells of the young stem tip are commonly binucleate, the nucleoli staining deeply with gossypimine. Solitary calcium oxalate crystals are scattered throughout the pith, phloem and inner cortex of the young stem; they are especially abundant in the pith of the young stem tip. Small starch bodies are plentiful in the pith, vascular tissue and inner cortex.

Secondary growth commences early, especially in fertile shoots, and follows the normal dicotyledonous pattern. The fascicular cambial tissue of the primary stem becomes linked by inter-fascicular cambium formed by a layer of medullary ray cells becoming meristematic.

A complete narrow ring of regular, thin-walled cambial tissue is thus formed, which cuts off secondary phloem tissue externally and secondary xylem internally. The rapid development of secondary xylem pushes outwards and compresses the secondary and primary phloem so that the latter tissues become indistinguishable from each other.

The vessels of the secondary wood tend to be cut off in radial series from the cambium and are interspersed with wood prosenchyma and intersected by numerous medullary rays.

Cork is formed immediately under the epidermis from the outermost cortical layer which assumes the function of a cork cambium, cutting off regular radial rows of rectangular corky cells to the outside (Fig. 24). In a stem showing several years' secondary growth the cortex, pericycle and phloem became greatly compressed and form the bark.

The Wood. The secondary xylem shows distinct annual growth rings due to the small tangentially-compressed prosenchyma and almost complete absence of vessels in the narrow zone of autumn wood.

In a transverse section of the wood (Fig. 25) the angular vessels are evenly distributed in radial clusters, long chains which may extend across an entire growth ring, or discontinuous radial rows, in a ground-work of tracheid-like wood prosenchyma intersected by numerous narrow medullary rays. The vessels are rather uniform in size, their tangential diameter

ranging from 25-30 μ .

The vessel elements are of medium length, averaging 500 μ , with oblique septa having simple or occasionally scalariform perforations.

The inter-vessel walls are perforated by numerous, generally crowded, bordered pits which are most frequently circular or elliptical in outline and 8-12 μ in diameter, showing a transitional tendency to vary through oblong to scalariform (Fig. 26).

Vessel-ray perforations are bordered on the vessel side only.

The wood prosenchyma is abundant; the elements are arranged in regular radial rows and are square to hexagonal and tracheid-like in cross-section, with wide lumina and rather thin walls. The diameter of the fibres varies from 8-20 μ ; wall thickness averages 2.5 μ . The individual fibres are rather short (400-750 μ) in length, non-septate and shortly-tapering at the ends. The pits in the walls are small, simple and scattered and are circular or elliptical in shape.

The medullary rays are numerous and narrow, being commonly uniseriate though occasionally 2 or 3 and rarely 4 or 5, cells in width. The rays vary considerably in depth from 3 to 100 cells. The end cells are longer than the rest of the cells of the ray and are tapering. (Fig. 27). The ray cells vary from 6-15 μ in breadth and 12-60 μ in depth.

Xylem parenchyma is completely lacking.

Starch bodies are abundant, especially during autumn, in the cells of the medullary rays and to a lesser extent in the fibres of the wood prosenchyma, which thus appears to take over in part the functions of storage parenchyma which is absent from the wood. Fig. 28 shows starch bodies filling the cavities of medullary ray cells and some prosenchymatous elements in a wood sample taken during autumn.

Harrar (1946) was unable to detect starch in the wood fibres of related genera but this may have been due to his samples not having been taken from the sapwood. *Vallea* was not examined by him.

The Root.

The root system of *Vallea stipularis* is much branched and woody with numerous fibrous rootlets.

The growing root tip is covered with a root cap of five layers of rather large, rectangular cells at its widest part at the tip, tapering to a single layer of cells a short distance behind the tip.

The active meristematic area of the young root is situated about 16 cell rows from the tip, (excluding the root cap). The cells of this area have the large nuclei characteristic of meristematic cells, some of which are in active mitotic division.

Behind the area of meristematic activity the tissue of the young root becomes differentiated into three primary tissues which later form the epidermal, cortical and stelar tissues of the older root. The

outermost layer or dermatogen has slightly radially elongated cells; the underlying periblem consists of 7 layers of isodiametric cells, while the central plerome is composed of vertically-elongated cells which are later differentiated into vascular elements.

A transverse section just behind the root-hair region (Fig. 30) shows the young root fully differentiated into external piliferous layer, cortex and central stele. The piliferous layer is composed of radially-elongated cells which in the root-hair region are drawn out into fine hairs. The cortex is wide compared with the small central stele which it surrounds, and consists of about 7 layers of large, rounded, thin walled parenchyma cells. Internal to the cortex is a single endodermal layer of small, rather thick-walled cells, slightly elongated tangentially. A single pericycle layer of small thin-walled cells lies internal to the endodermis.

The stele of the young root is commonly tetrarch, containing 4 small phloem masses situated external to small groups of protoxylem elements scattered throughout a central medulla of small parenchymatous cells.

Secondary growth begins early as in the stem, and fine rootlets of as little as 1 mm. diameter consist largely of secondary xylem.

A root of one or more years' secondary growth (Fig. 31) consists largely of a solid central core of secondary xylem surrounded by cambium, narrow phloem

and a narrow cortex containing numerous irregular groups of fibres. Cork forms early in the outermost layer of the cortex.

The cortex shows no differentiation into an outer and inner zone as in the stem but consists of uniform, rather small-celled parenchymatous tissue which becomes less compressed by the increase in the central core of xylem than does the cortex of the stem. This is due to numerous groups of strengthening fibres scattered throughout the cortex, some of which extend to immediately below the external corky layers. The fibres are not confined to a pericyclic ring but are of the same structure as those of the stem.

The secondary xylem of the root (Fig. 32) differs in several respects from that of the stem. Its texture is more open and less compact due to the greater part of its bulk being composed of vessel elements with wide lumina. Annual growth rings are not distinct as in the stem wood; the wood prosenchyma is flattened tangentially in the narrow zone of Autumn wood but the presence of small vessels breaks the continuity of the denser ring thus formed.

The vessels are not distributed in regular series or clusters but are irregularly scattered in short chains of 3 or 4 elements, in pairs, or singly. They show a very great variation in size, ranging in cross-sections from hardly larger than a prosenchymatous element to very large; their tangential diameter ranges from 16 to 75 μ .

Wood prosenchyma is less abundant than in the stem as the vessels occupy the greater bulk of the wood. The prosenchymatous elements closely resemble those of the stem, their tangential diameter having a similar small range of 5-20 μ .

Medullary rays are rather less numerous than in the stem and are commonly uniseriate and occasionally biseriate.

Xylem parenchyma is again completely lacking.

SYSTEMATIC POSITION OF VALLEA.

It is evident, from a review of the taxonomic history of the genus *Vallea*, that there has been no difference of opinion among the various authorities as to its systematic position within the natural order *Tiliaceae*, in its widest sense, and its especial affinities with a distinct section of the order which, though its generic content has varied slightly according to different authors, has remained essentially the same throughout the various classifications. This is the *Heteropetalae* of Bentham and Hooker and the *Elaeocarpeae* (or *Elaeocarpaceae*) of other authors. Opinions have differed, however, as to the nearest affinities of *Vallea* within the section.

The genera which have been most consistently included within this group are *Elaeocarpus* L., *Sloanea* L., *Vallea* Mutis, and *Aristotelia* L'Herit., other genera included by various authors are *Tricuspidaria* Ruiz et Pav., *Echinocarpus* Blum., *Crinodendron* Mol., *Dubouzetia* Panch., and *Antholoma* Labill. Bentham and Hooker added *Prockia* L., *Hasseltia* H.B.K., and *Plagiopteron* Griff. as the tribe *Prockieae*.

De Candolle separated the group as the order *Elaeocarpaceae* on the floristic grounds of divided petals and linear, apically-dehiscent anthers. Bentham and Hooker distinguished it from the remainder of the *Tiliaceae* as the second series *Heteropetalae* characterised by "absent, sepaloid or divided, rarely truly

petaloid, petals, never contorted in the bud". Only their Tribe Prockieae and the genus *Sloanea* possess sepaloïd or no petals and lobing of the petals, though frequent, is not universal; they are occasionally entire in *Aristotelia* and always entire in *Dubouzetia*. The only constant floristic feature throughout the group (with the exception of the Prockieae) is the linear anther with apical porose dehiscence.

In the possession of a torus which is not elongated between the insertion of the perianth and androecium and of an hypogynous annular disc in which the stamens are inserted, *Vallea* resembles *Sloanea*, *Echinocarpus* and *Antholoma* and differs from *Elaeocarpus* and *Aristotelia*. On this account it is united with the three former genera in the Tribe Sloanieae by Benthams and Hooker. The torus of *Elaeocarpus* is more or less elongated between the insertion of the perianth and androecium; that of *Aristotelia* is cup-shaped and the perianth and androecium are perigynous.

Apart from the shape of the torus the flower of *Vallea* bears a greater resemblance in its parts to that of *Aristotelia* (with which it is united in the Tribe Aristoteliaceae by Engler and Prantl) than to that of *Sloanea*. In most respects the flowers of *Vallea* and *Aristotelia* are similar, both possessing a calyx of free sepals, a corolla of divided petals (which may be occasionally entire in *Aristotelia*), numerous stamens and 2 ovules in each loculus of the ovary.

Separation of the Elaeocarpaceae from the Tiliaceae.

Engler and Prantl, following the example of Szyszyłowicz (1885) used mainly anatomical characters to separate the 'Elaeocarpaceae' from the Tiliaceae, and it is by their anatomy that the former group is most sharply differentiated.

Dumont (1887) after a comprehensive study of the comparative anatomy of the Malvales came to the conclusion that "the characteristic structure of the Malvales is more degraded in the Heteropetalous Tiliaceae than in any other group". The 'Heteropetalous Tiliaceae' include the 'Elaeocarpaceae' of Engler and Prantl and the Tribe Prockieae of Bentham and Hooker. The latter group shows a few anatomical features characteristic of the Holopetalous Tiliaceae but its general anatomy is consistent with that of the Heteropetalae. The possession of globose longitudinally-dehiscent anthers sets it apart floristically from the Elaeocarpaceae of Engler and Prantl.

The Elaeocarpaceae (of Engler and Prantl) differ from the Tiliaceae in the following anatomical features:-

(1) The epidermal covering. Epidermal hairs are infrequent among the Elaeocarpaceae; when present they are small and usually unicellular. The leaf hairs of *Vallea stipularis* are characteristic of the group. Hairs are abundant throughout the Tiliaceae and are commonly multicellular and peltate or capitate or variously branched.

(2) Secretory products. Mucilage is lacking in the Elaeocarpaceae. Mucilaginous epidermal cells are described by Szyszyłowicz (19) in the leaves of a few genera but this is the only record of their occurrence. They are not present in *Vallea stipularis*.

Mucilaginous cells and lysigenous mucilage canals are present in the pith and cortex of all Tiliaceae with the exception of the genus *Muntingia*.

Gum-secreting cells are described by Szyszyłowicz in the bast of certain Prockieae which in this feature resemble the Tiliaceae. Gum is absent from the Elaeocarpaceae.

The occurrence or absence of secretory elements is perhaps the most striking anatomical difference between the two families.

(3) Excretory products. Calcium oxalate occurs among the Elaeocarpaceae in the form of small, solitary, rhomboidal crystals, sparsely distributed in pith and cortex (as in *Vallea stipularis*). Crystals are generally abundant in the Tiliaceae where they are often aggregated in clusters.

Tannin. In the Elaeocarpaceae, according to Dumont, this excretory product often invades the parenchyma, medullary rays and pith where it often fills elements arranged in longitudinal rows. It is not found in this position in *Vallea stipularis*.

(4) Petiolar structure. According to Dumont the petiolar bundles of the Elaeocarpaceae form a more or

less open arc, bicollateral medullary bundles never being present. In the Tiliaceae they form either an open or closed circle which gives rise by invagination to bicollateral medullary bundles. The petiolar vascular system of *Vallea stipularis* takes the form of a closed circle for most of the length of the petiole, opening out into an arc at base and apex and invaginating to give collateral medullary bundles.

The appearance of the vascular strand in cross-section varies greatly according to the level of the petiole at which the section is taken, and a series of sections from base to apex is necessary to ascertain whether the vascular strand ever closes into a complete circle. The vascular system of the petiole of *Vallea* is therefore probably not as anomalous as it would appear from Dumont's observations on related genera.

(5) Cortical structure. The fibrous strengthening tissue of the cortex is poorly developed in the Elaeocarpaceae in contrast to the Tiliaceae. In the latter the groups of phloem ('bast') are bounded toward the primary cortex by bands of fibres. In the Elaeocarpaceous genera *Elaeocarpus* and *Vallea* and in *Prockia* and *Hasseltia* of the Prockieae the bands are replaced by small groups of fibres in a more or less interrupted pericyclic ring. The secondary bast in Tiliaceae is well stratified by bands of bast fibres, and is also well-developed in *Aristotelia* but in other Elaeocarpaceae it is very poorly-developed,

containing only scattered fibrous elements in *Elaeocarpus* and none in other genera.

(6) Wood structure. The secondary xylem of the *Elaeocarpaceae* differs in several respects from that of the *Tiliaceae*. A detailed study of the woods of the two families has been carried out by Kukachka and Rees (1943). These authors consider that nearly all the characters of the wood of the *Elaeocarpaceae* point to a structure more primitive than that of the *Tiliaceae*. The wood of *Tiliaceae* has none of the following features which are characteristic of the wood of *Elaeocarpaceae*:-

- (1) long vessel - members.
- (2) circular to scalariform pitting of the vessels.
- (3) oblique perforation plates which are mostly simple but show vestiges of the scalariform condition
- (4) parenchyma generally lacking
- (5) wood prosenchyma fibres very tracheid-like in cross-section

The wood of *Vallea stipularis* shows all the above characters. Parenchyma is completely lacking.

The only advanced character in the wood of *Elaeocarpaceae*, according to Kukachka and Rees, is the presence of septate wood fibres in most of the genera examined. They are not present in the wood of *Vallea stipularis*.

The above authors did not examine the wood of the *Prockieae*; their '*Elaeocarpaceae*' was that of

Engler and Prantl. They came to the conclusion that "the evidence from wood anatomy substantiates the arrangement of Engler and Prantl"; that is, the segregation of the Elaeocarpaceae from the Tiliaceae and making it a distinct family. Using only the characters of the secondary xylem they arrived at an arrangement of the genera within the family which is essentially that outlined by Engler and Prantl, dividing them into two tribes. The tribe Elaeocarpaceae is placed before the Tribe Aristoteliaceae because of its longer vessel members and solitary arrangement of vessels. These characters are considered 'primitive' by Kukachka and Rees. The Tribe Aristoteliaceae, consisting of the two genera *Vallea* and *Aristotelia*, has much shorter vessel-members and vessels generally arranged in radial multiples and clusters.

The woods of the two genera are very similar except that *Vallea* has longer vessel-members and scalariform pitting, features which place it before *Aristotelia* according to the standard of relative primitiveness used by Kukachka and Rees.

Other workers on wood anatomy have arrived at a similar conclusion to that of the above authors. Chalk (1942) for example, in a discussion of the taxonomic value of wood anatomy, states that "in the group of orders Tiliales, Sterculiales and Malvales it is easier to place a wood in the whole group, if Elaeocarpaceae be excluded, than to assign it to any one family" and "among tribes that are distinct are

the Sterculieae and the Elaeocarpeae, and the raising of these to the rank of families is fully backed by their wood anatomy".

Conclusion.

The differences between the Elaeocarpaceae and the Tiliaceae are mainly anatomical and are sufficient to justify the separation of the former group as a distinct family. The generic composition of this family is that outlined by Engler and Prantl.

The Prockieae are an anomalous group, anatomically similar to the Elaeocarpaceae except for the presence of the gum-secreting cells in the bast; floristically they lack the linear anthers characteristic of this family. The possession of the secretory elements and anthers typical of Tiliaceae exclude them from the Elaeocarpaceae. They can best be regarded as a reduced type of Tiliaceae.

Vallea appears to stand closest to Aristotelia in anatomical features. The secondary xylem of the two genera shows marked similarities. Floristically Vallea resembles Sloanea in the shape of the torus but otherwise is similar to Aristotelia.

In its natural distribution along the Andean mountain range Vallea stands midway between Sloanea and Aristotelia. The former genus of 45 species is distributed east of the Andes in tropical South America; the latter, with only ten species, is found west of the Andes in Chile, New Zealand and Tasmania.

This intermediate geographical position of *Vallea* is interesting but it is not suggested that the genus is transitional between *Sloanea* and *Aristotelia*. The floral differences from the former genus are too great. It is possible that *Vallea* and *Aristotelia* have a common ancestry in view of their anatomical similarity; divergence has taken place in the shape of the torus of the flower.

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VALLEA STIPULARIS Linn.f.

FIGURES.

Fig. 1 Inflorescences. X 1.

Fig. 2 Flower. Vertical section X 5.

f incurved filaments
d staminal disc

Fig. 3 Floral diagram.



Fig. 1

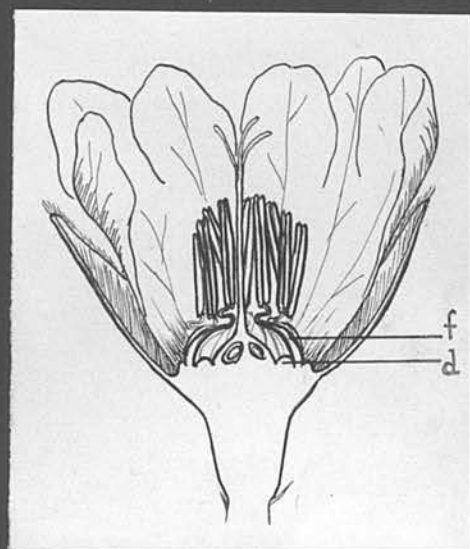


Fig. 2

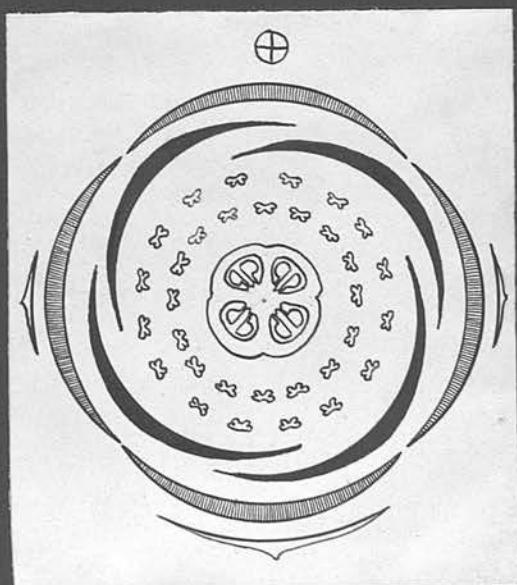


Fig. 3

Fig. 4 Sterile branchlets. X 1.

Fig. 5 Flower bud. T.S. at anther level X 10.
showing valvate aestivation of sepals,
imbrication of petals and numerous stamens.
This flower shows pentamerous symmetry.

Fig. 6 Flower bud. T.S. at ovary level X 20.
showing tetramerous symmetry.
d darkly stained tissue of staminal disc.

Fig. 7 Stamen. X 10.

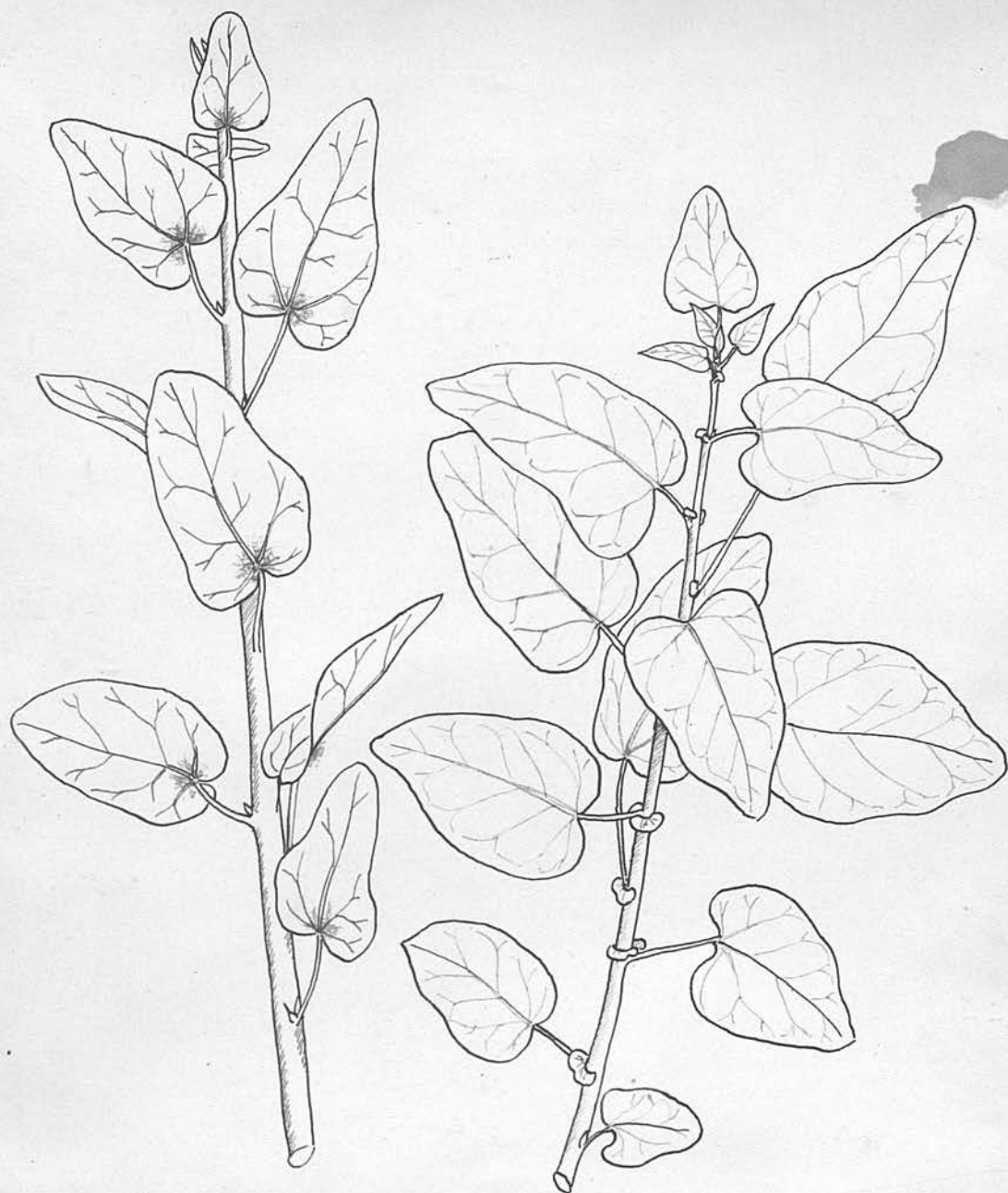


Fig. 4

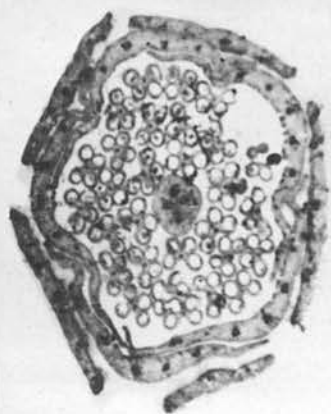


Fig. 5

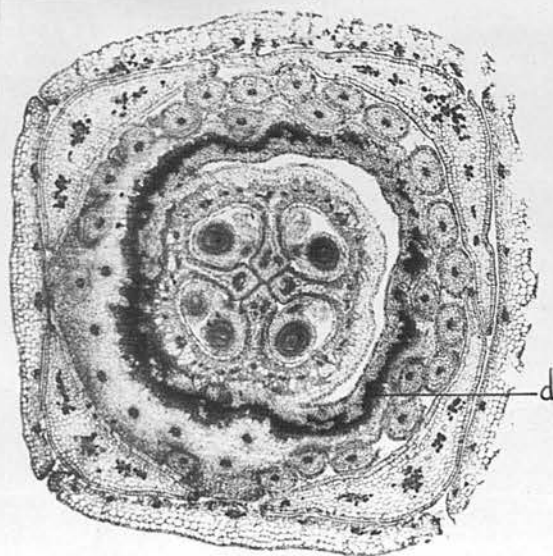


Fig. 6

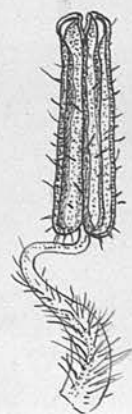


Fig. 7

- Fig. 8 Anthers at tetrad stage. T.S. X 35.
Note the four-lobed style.
- Fig. 9 Mature anthers. T.S. X 35.
- Fig. 10 Mature anther. T.S. X 130.
showing epidermal hair.
- Fig. 11 Gynaecium. X 10 from tetramerous flower
with perianth and androecium removed.
Note the crenulate staminal disc (d).
- Fig. 12 Ovary. T.S. centre X 40.
showing four carpels imperfectly fused at
their margins, and two ovules in each loculus.
In the lower loculus only the funicle of the
second ovule is visible.
- Fig. 13 Ovary. T.S. near apex X 40
showing one ovule and the funicle of another
in each loculus.

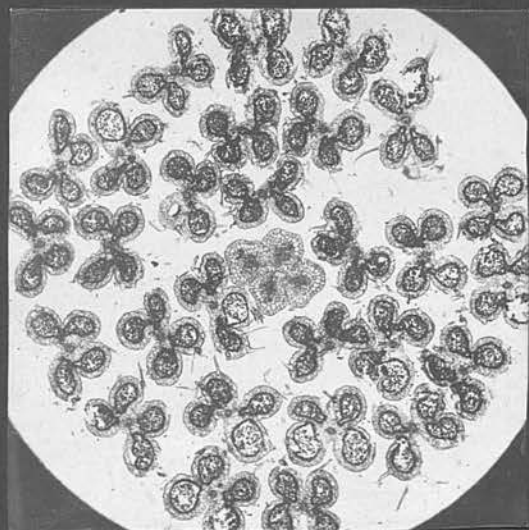


Fig. 8

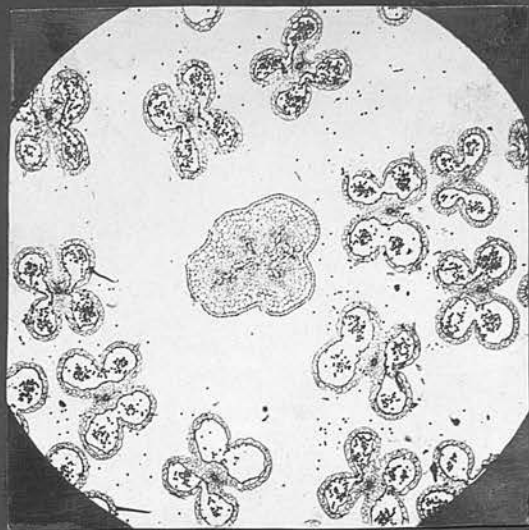


Fig. 9

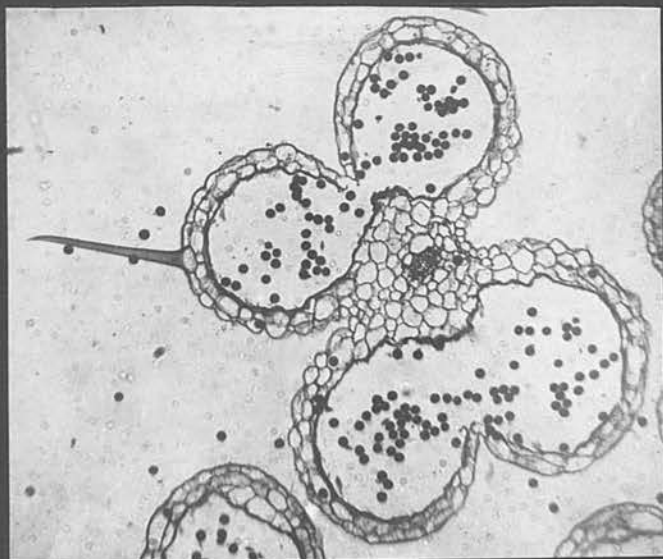


Fig. 10

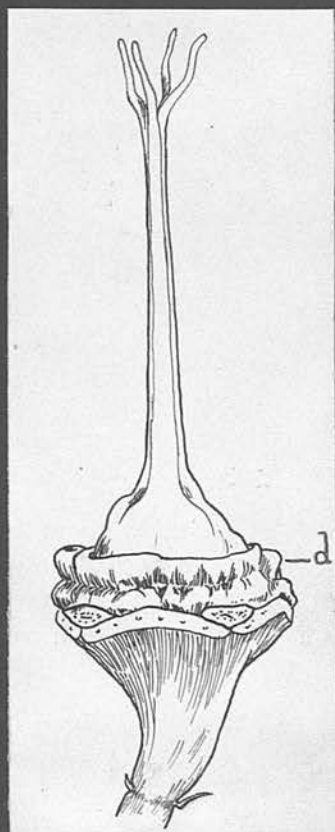


Fig. 11

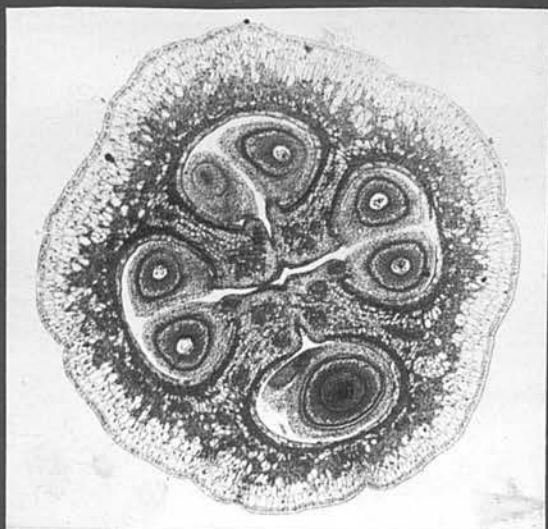


Fig. 12

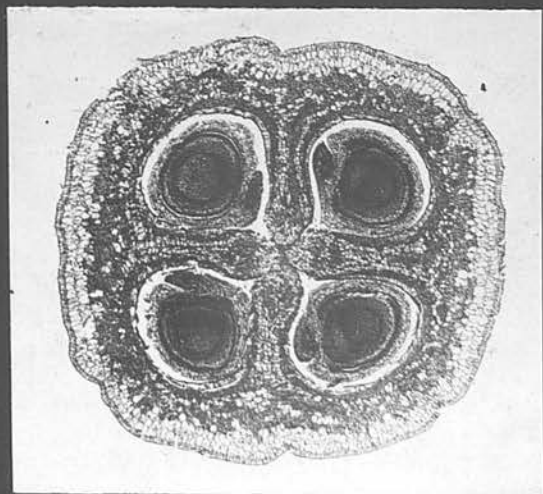


Fig. 13

Fig. 14 Ovary. L.S. X 40.

Showing axile placentation of the ovules.

Fig. 15 Fruit wall. L.S. X 25.

Showing a fleshy tubercle on the outer surface and the thick endocarp.

Fig. 16 Seed. L.S. X 10.

t testa
e endosperm
c cotyledon of embryo
a aril

Fig. 17 Upper epidermis of leaf. Surface view X 450.

Fig. 18 Lower epidermis of leaf. Surface view X 450.

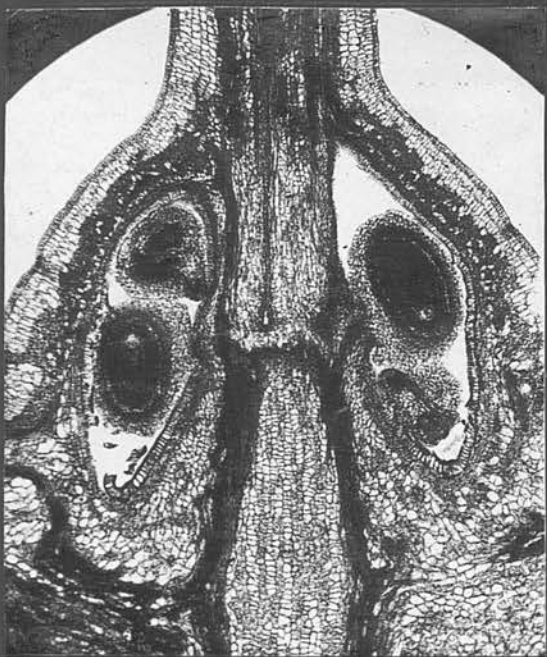


Fig. 14

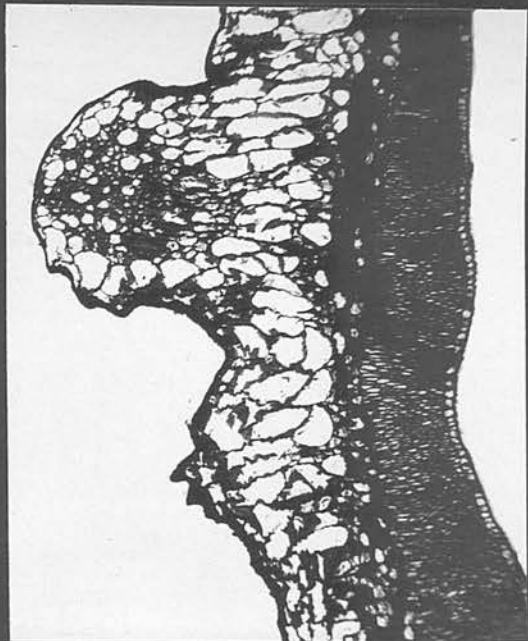


Fig. 15

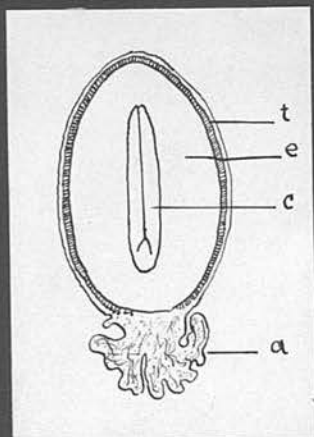


Fig. 16

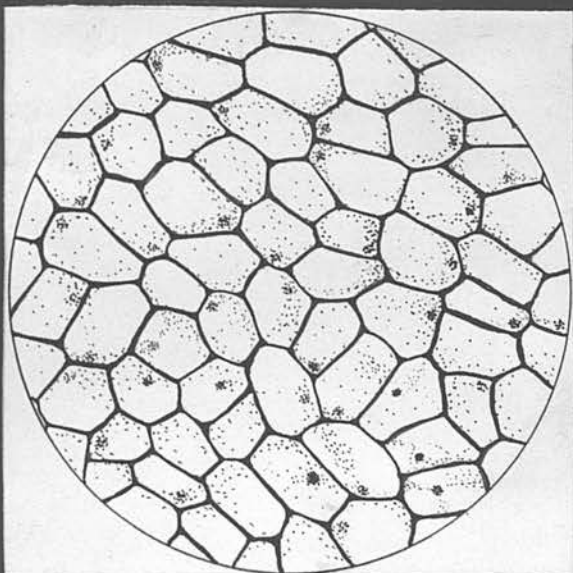


Fig. 17

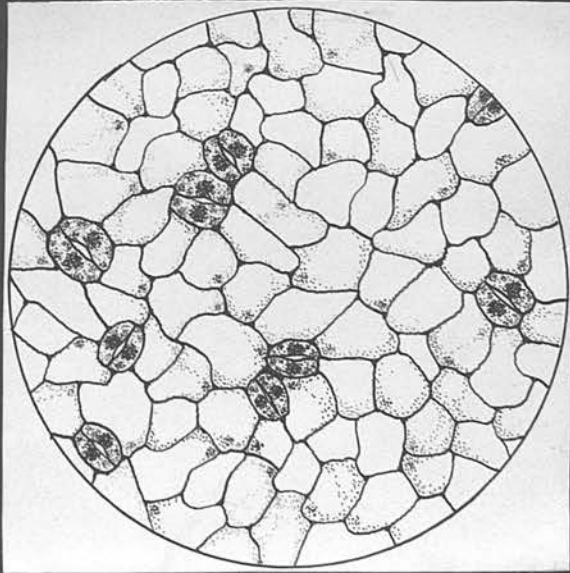


Fig. 18

Fig. 19 Leaf lamina. T.S. X 300.

showing a lateral vein. Note the papillation
of the lower epidermis.

Fig. 20 Midrib of leaf. T.S. X 130.

x xylem
ph phloem

Fig. 21 Petiole. T.S. centre X 50.

showing a closed cylinder of vascular tissue
and a small medullary bundle.

x, ph xylem and phloem of medullary bundle.
c crystals in cortex and pith.

Fig. 22 Cortex of primary stem. T.S. X 300.

showing pericyclic fibres.

Fig. 23 Secondary stem. T.S. X 35.

showing one year's secondary growth.

f pericyclic fibres
ph phloem
c cambium
x secondary xylem
px protoxylem
m medulla or pith

Fig. 24 Cortex of secondary stem. T.S. X 200.

showing cork formation from sub-epidermal
layer and fully-formed pericyclic fibres.

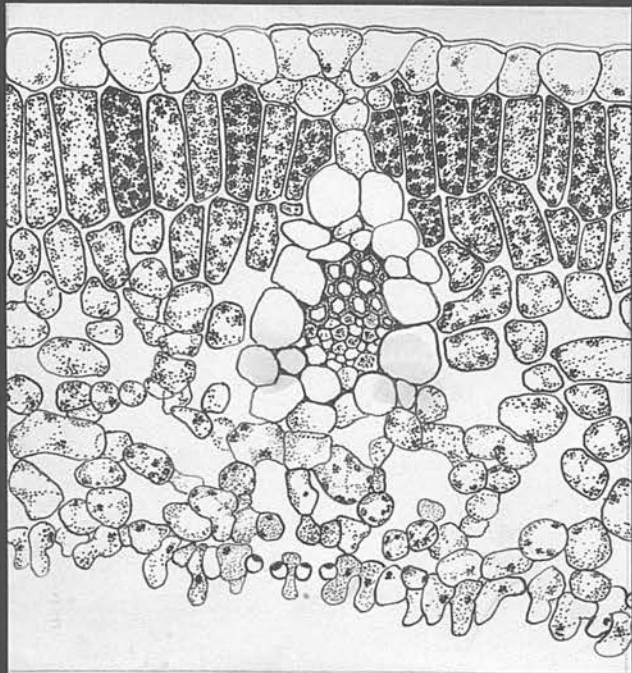


Fig. 19

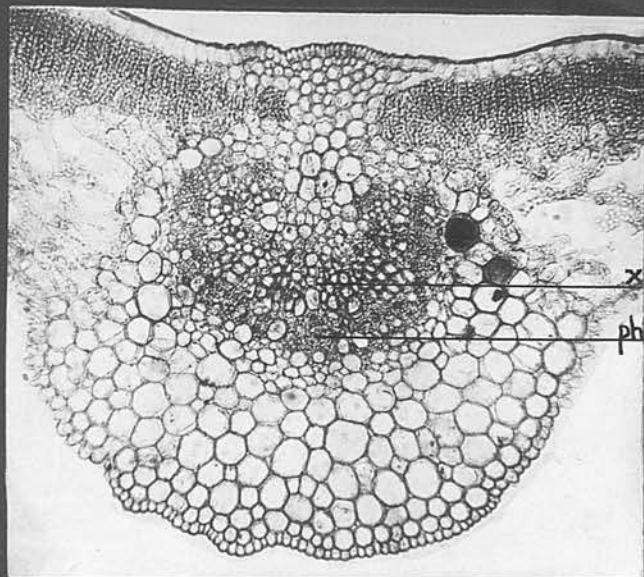


Fig. 20

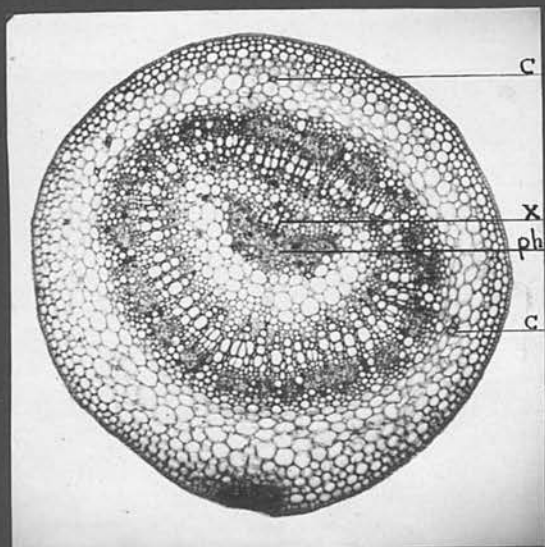


Fig. 21

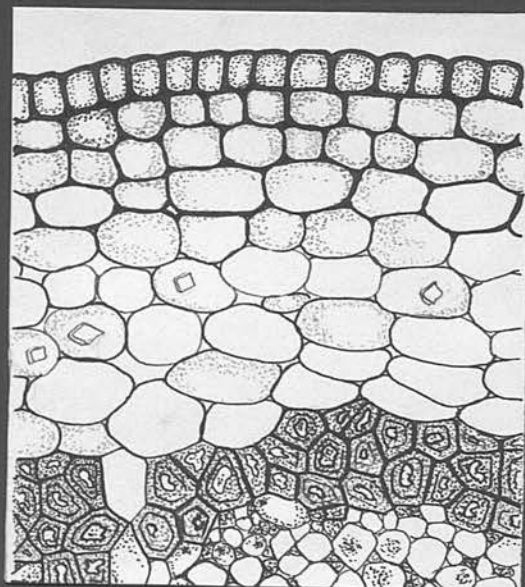


Fig. 22

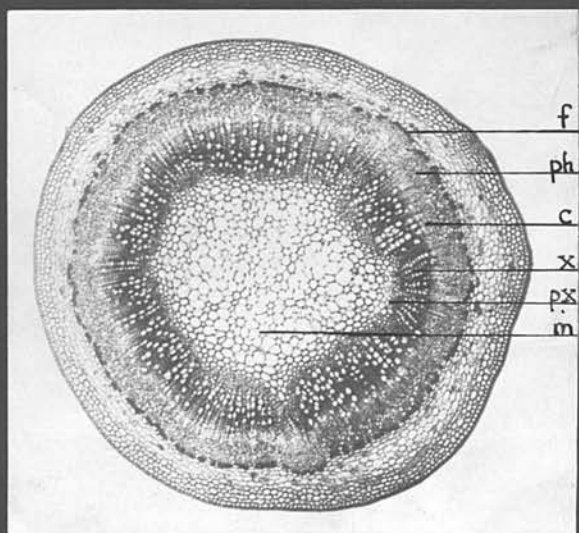


Fig. 23

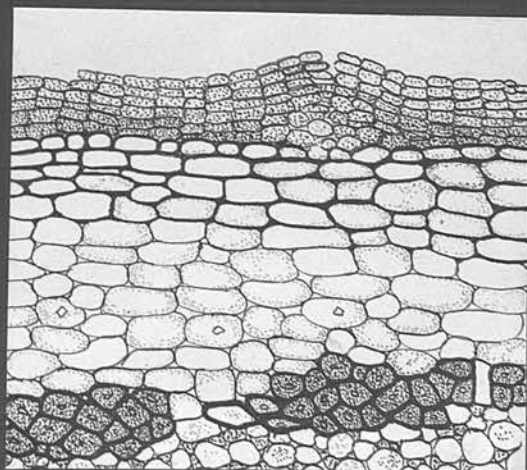


Fig. 24

Fig. 25 Secondary xylem. T.S. X 130.

Fig. 26 Xylem vessels. L.T.S. (diagrammatic) X 450
showing various types of pitting. Circular
bordered pits show a transition through
elliptical to scalariform.

Fig. 27 Secondary xylem. L.T.S. X 130
showing numerous medullary rays.

Fig. 28 Secondary xylem. L.R.S. X 70.
Ray cells and some wood prosenchyma are filled
with darkly-stained starch bodies.

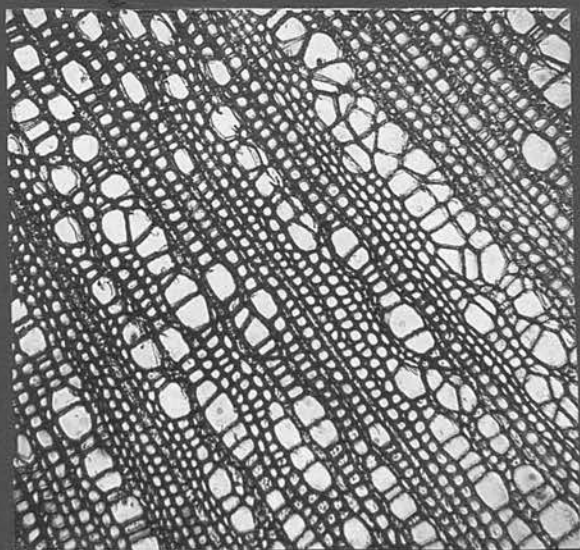


Fig. 25

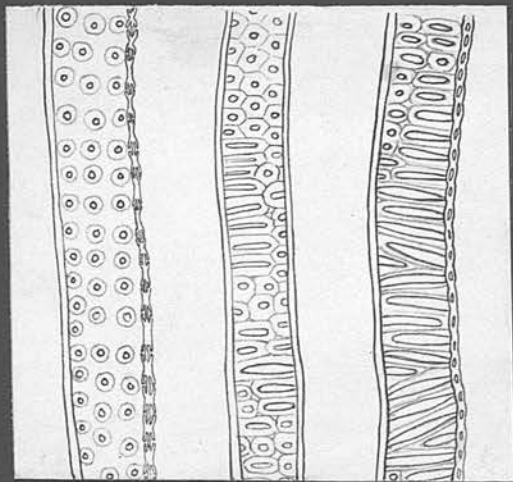


Fig. 26

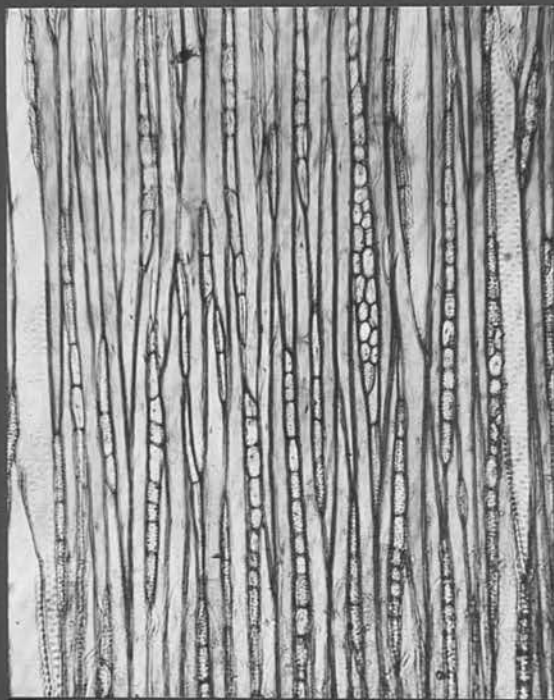


Fig. 27

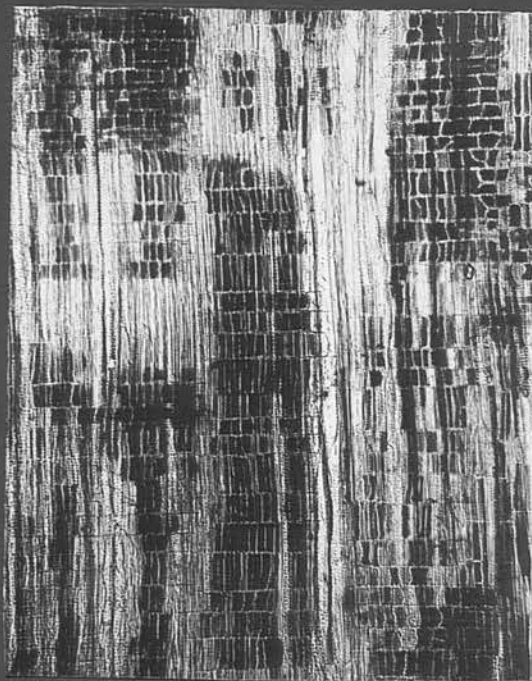


Fig. 28

Fig. 29 Secondary xylem. L.R.S. X 300

showing a medullary ray traversing vessels
and wood prosenchyma.

Fig. 30 Primary root. T.S. X 100.

px protoxylem

Fig. 31 Secondary root. T.S. X 100

showing great development of secondary xylem.

Fig. 32 Secondary xylem of root. T.S. X 130.

Medullary rays and wood prosenchyma are filled
with darkly-stained starch bodies.



Fig. 29

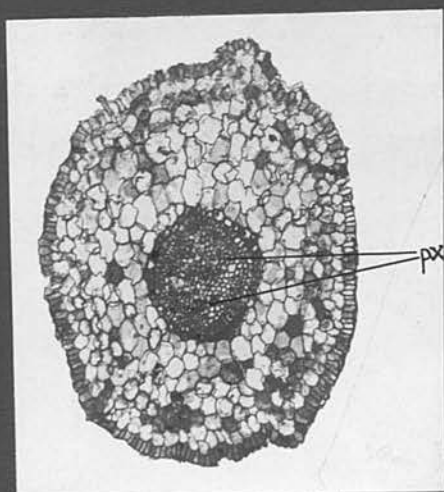


Fig. 30

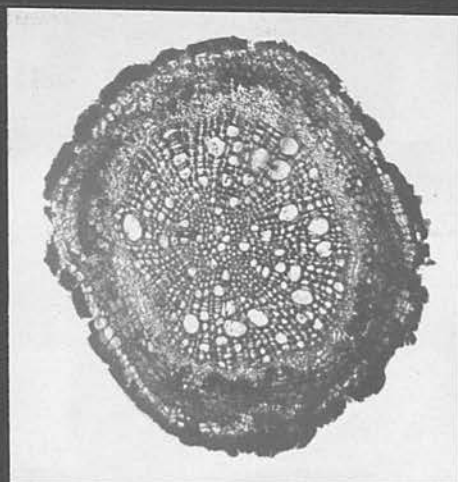


Fig. 31.

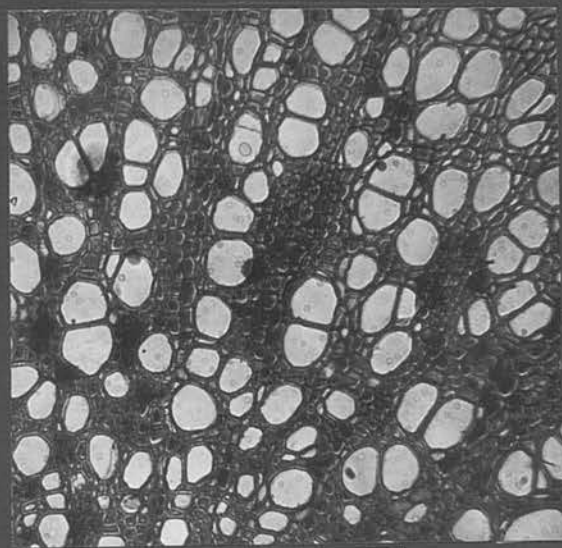


Fig. 32

THE GENUS HARTIA, DUNN.

Hartia is a genus of the Ternstroemiaceae endemic to eastern Asia, with its centre of distribution in southern China.

The natural habitat of the species of this genus is mixed forest or oakwood in valleys and ravines at altitudes ranging from 2,000 to 3,500 metres. They are evergreen trees reaching, according to Lee (1935) a height of 14 metres, with smooth slender trunks up to 40 cm. in diameter and slender horizontal branches. The leaves are simple, lanceolate, dark green and glossy; the white flowers are borne singly in the leaf axils. The most outstanding feature common to all species of the genus is the curious winged petioles which enclose the buds and the growing point of the stem.

A fine plant of the species Hartia Sinensis Dunn (Fig. 1) flowered for the first time in this country in the Royal Botanic Garden, Edinburgh, in 1945 and again, very profusely, in 1948. It was thought worth while to investigate the general features of this little-known Chinese plant.

Taxonomic history of the family Ternstroemiaceae.

The first recognition of the Ternstroemiaceae (or Theaceae) as a natural group was made by Anthoine de Jussieu (1789) when he differentiated the genera Thea, Ternstroemia and Camellia, as a section characterized

by their dry, many-seeded fruits, from the remaining genera of his "Order Aurantia". This Order, "les Orangers", was chiefly a combination of Rutaceae and Ternstroemiaceae, and included the genus *Citrus*.

Mirbel (1813) established the Ternstroemiaceae as a separate family with 13 genera. De Candolle (1824) split the family into two - Ternstroemiaceae with 13 genera, Camelliaceae with *Camellia* and *Thea*. Cambessedes (1838) reunited the two groups into a single family, adding 2 genera to the original 13, but retaining several anomalous genera, including *Venevattia* (Bixaceae). The family took on its modern form when revised by Endlicher (1842). Bentham and Hooker (1862) admitted 31 genera plus 13 "genera affinia et dubia". Melchior (1925) reduced the number to 23.

Taxonomic history of the genus *Hartia*, Dunn.

The genus *Hartia* was established by Dunn (1905) from material collected by A. Henry in Yunnan province, China, and is named in honour of Sir Robert Hart, Inspector-General of the Chinese Maritime Customs at that time.

Dunn noted the close affinity of his new genus with the genera *Stuartia* Linn., and *Schima* Reinw. Evidence for the relationship of *Hartia* to these genera will be considered at the end of this paper. The new genus was placed alongside *Stuartia* and *Schima* in Bentham and Hooker's tribe Gordonieae of the

Ternstroemiaceae. This tribe was separated from the remaining 5 in the family by the characters of versatile anthers and scanty endosperm. Melchior (1925) separated *Hartia* and *Schima* from *Stuartia* and *Camellia* as sub-tribes of the tribe *Camellieae*, on account of their winged seeds and small calyx.

Synonymy.

Material collected from the Yunnan province of China formed the basis for the establishment of the genus *Hartia*. The single species *H. sinensis* was described as a tree with alternate, simple, leathery leaves, boat-shaped petioles and white flowers solitary in the leaf axils. Dunn (1905) gives a full description of the plant and a good figure.

The genus remained monotypic until 1934 when a Chinese author described two new species. Four more species were subsequently added, two of which are very similar to, and probably mere forms of, *H. sinensis*. These are *H. yunnanensis* Hu (1935) from a ravine, Yunnan, and *H. serratisepala* Hu (1938) from mixed oak-woods, South-west Yunnan. The former "species" differs from the typical *H. sinensis* only by its smaller fruits and sepals, the latter by its glabrous leaves. Both these so-called "species" have evidently been described from isolated herbarium specimens which happened to vary slightly from the type.

Of the four other species described the most

distinct is H. robusta Hu (1937) which "differs from all other known species in the resinous- glandular-lepidote investiture on branches, under-surface of leaves and sepals, and in its much larger fruits." No locality is given by the author. H. kwangtungensis Chun, (1934) from the province of Kwangtung, also has pubescent leaves and persistent indumentum on stem and petiole. It is possible that H. robusta Hu is synonymous with this species. H. micrantha Chun (1934) also from Kwangtung province, is separated on account of its small flowers, rounded sepals and distinct leaves with obscure lateral veins. H. tonkinensis Merrill (1938) from Indo-China, is the only species so far recorded outside China. It is very similar to H. micrantha of Kwangtung province.

Uses and Cultivation.

No species of *Hartia* is in general cultivation in this country. It is doubtful whether the plant is put to any use in its native country as it does not appear to be well-known and never attains the dimensions of a timber tree.

Material.

Material for this work was obtained from a well-grown plant of Hartia sinensis Dunn. growing in the glasshouses of the Royal Botanic Garden, Edinburgh. Raised from seed collected in China by George Forrest in 1925, it has grown into a small tree 5 m. in height

with a stem diameter of 5 cm. HAIRY DUNE.

Tree, 7 to 15 m. Methods. Trunk up to 30 cm.

For methods of fixation, sectioning and staining of the material see previous paper on *Steriphoma*.

Leaves brown pubescent when young. Leaves alternate, leathery, evergreen, ovate-lanceolate, tapering toward apex but apex obtuse, margin sharply dentate with up-curving teeth. Laminas 5-13 cm. long, 3-4 cm. broad. Petioles short, 1-1.5 cm. covered with long silky hairs, winged, the folded wings enclosing bud in leaf axil or stem apex. Flowers solitary in leaf axil, on short stout pedicels, 5 cm. across. Bracteoles 2, small. Sepals 5, unequal, about 1.5 cm. long, joined at base, acuminate, dentate, pubescent outside, reflexed in open flower, persistent and erect in fruit. Petals 5, broad, white, longer than sepals, joined at base with each other and with base of tube formed by fused stamens. Filaments, covered with long silky pubescence outside, rather reflexed in open flower. Stamens numerous, 60-70, filaments fused for $\frac{2}{3}$ of their length into an erect tube, anthers versatile, extrorse, pollen yellow. Ovary of 5 fused carpels, sessile, superior, stigmas 5. Ovules 4 in each loculus, superposed. Fruit acuminate, woody. Seeds flattened, narrow-winged.

The Flower.

The flower of *Haeria* is hermaphrodite and hypogynous.

Floral formula $\text{SS, OS, 4(2), 3(1)}$

HARTIA SINENSIS DUNN.

Tree, 7 to 13 m. in height, trunk up to 30 cm. diameter, bark grey, smooth. Branches horizontal, glabrous. Branchlets brown, slender, clothed with brown pubescence when young. Leaves alternate, leathery, evergreen, ovate-lanceolate, tapering toward apex but apex obtuse, margin sharply dentate with up-curving teeth. Lamina 6-13 cm. long, 3-4 cm. broad. Petiole short, 1-1.5 cm. covered with long silky hairs, winged, the folded wings enclosing bud in leaf axil or stem apex. Flowers solitary in leaf axil, on short stout pedicels, 3 cm. across. Bracteoles 2, small. Sepals 5, unequal, about 1.5 cm. long, joined at base, acuminate, dentate, pubescent outside, reflexed in open flower, persistent and erect in fruit. Petals 5, broad, white, longer than sepals, joined at base with each other and with base of tube formed by fused stamen filaments, covered with long silky pubescence outside, rather reflexed in open flower. Stamens numerous, 60-70, filaments fused for $\frac{2}{3}$ of their length into an erect tube, anthers versatile, extrorse, pollen yellow. Ovary of 5 fused carpels, sessile, superior, stigmas 5. Ovules 4 in each loculus, superposed. Fruit acuminate, woody. Seeds flattened, narrow-winged.

The Flower.

The flower of *Hartia* is hermaphrodite and hypogynous.

Floral formula $K_5, C_5, A(\infty), G(\underline{5})$

The calyx is not protective in the bud, this function being assumed by the corolla. In the open flower the sepals are reflexed (see Fig. 2) but persist into the fruiting stage and then become erect (Fig. 3). They are slightly unequal in size, the posterior sepal being the largest and overlapping the two adjacent sepals (see Figs. 4 and 5). The internal structure is very simple. A papillose epidermis on both inner and outer sides enclose several layers of undifferentiated parenchyma. Hairs on the outer surface are non-septate, thick-walled, and have a swollen base in the hypodermal layer. 5 main vascular strands in each sepal give rise to numerous lateral strands.

The corolla assumes the protective function of the calyx in the bud. One of the posterior petals is very large and curved, overlapping the adjacent petals in the flower (see Fig. 4) and completely enclosing all 4 petals in the bud (see Fig. 5). In the open flower the petals curve backwards exposing the erect tube formed by the fused stamen filaments (see Figs. 1 and 2). Internal structure of the petals is very simple and similar to that of the sepals. The vascular supply consists of 8 to 12 strands which branch freely.

The androecium consists of 60 to 70 stamens whose filaments are fused for $\frac{2}{3}$ of their length into an erect tube joined to the corolla at its base. The anthers surround the style and stigmas (see Fig. 5). The free upper portion of each filament tapers toward its apex

which is attached to the centre of the anther connective (Fig. 6). From the position of the vascular strands in 2 concentric rings in cross-sections of the staminal tube the stamens appear to arise in 2 series. In T.S. the filaments show a papillose epidermis and a single vascular strand. Each anther contains 4 pollen-sacs and shows a normal internal structure (Fig. 7). An endothelial layer with spiral and longitudinal bands of thickening on the cell walls surrounds each pollen sac, and this type of strengthening is also present on the cells of the tissue between the pollen sacs and the centre of the connective.

Dehiscence occurs by a longitudinal split along the groove between each pair of pollen sacs. This region is occupied by a line of large empty cells with spiral bands of thickening on their walls, forming a well-defined stomium (Fig. 8). The mature anther loses water rapidly and, the contraction of the epidermal cells being greater than that of the endothelial cells with their strengthening bands, a tension develops and a split occurs along each side of the stomium where the endothelial cells are without strengthening bands. The pollen sac walls spring outwards thus setting free the pollen (Fig. 9). The grains are yellow in the mass; individually they are hyaline and oval in shape.

The gynaecium is composed of 5 carpels fused to form a quinquelocular ovary, simple style and 5 stigmatic lobes. At the base of the ovary the carpels are

completely fused; their margins, which form the central column and bear the ovules, separate at the centre of the ovary (Fig. 11) and up the style, eventually becoming completely free to form the stigmatic lobes (Fig. 10). The upper (inner) surfaces of the stigmatic lobes are receptive and the conducting tissue of elongated cells continues, in diminished quantity, down the style, becoming confined to the carpel margins. The ovary tissue is uniform parenchyma. Stomata are present in the outer epidermis; none were observed in the epidermis lining the ovarian cavities.

Four erect anatropous ovules are present in each loculus borne in two superposed pairs on the carpel margins (see Fig. 3). The ovules are large and compressed, with a flattened margin which later develops into the membranous wing of the seed (Fig. 3). The embryo sac is prominent and is surrounded by abundant nucellus tissue. The epidermal layer of radially-elongated cells is very distinct in sections (Fig. 12).

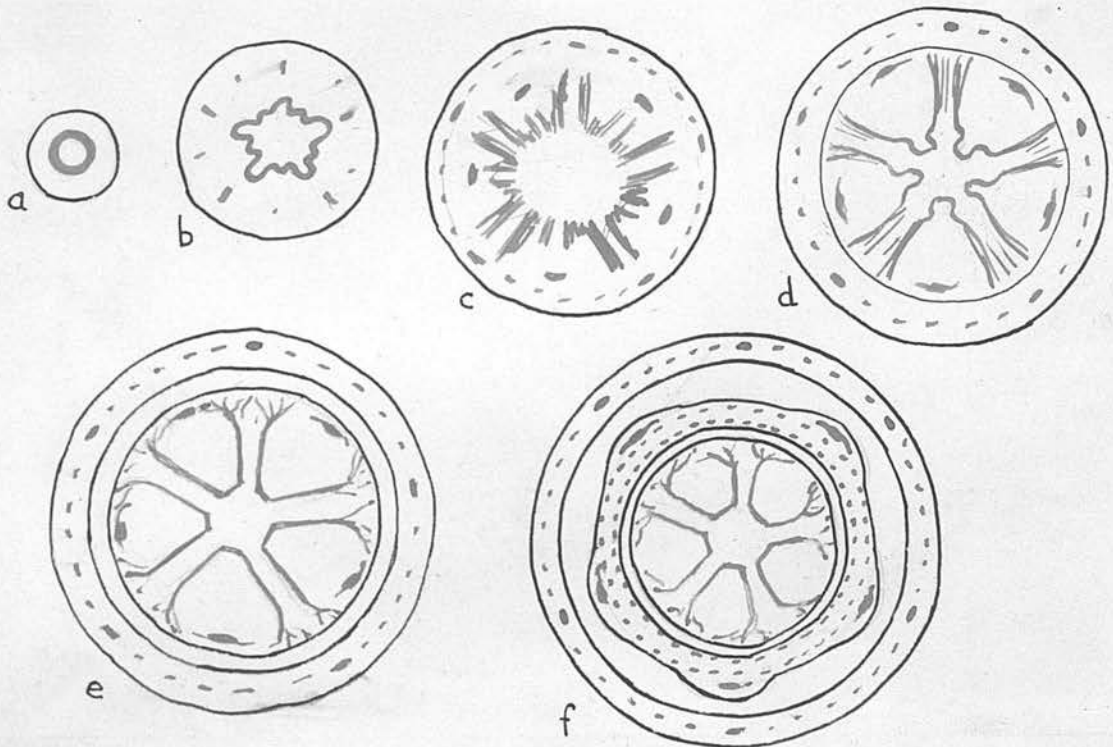
Fruit and Seed.

Both fruit and seed proved extremely difficult to section because of their hard brittle texture. During maturation of the fruit the cells of the ovary tissue become tougher-walled and lose their contents. The vascular bundles increase in size and their associated secretory cells become prominent showing dense contents; they are also present in the central axis (see Fig. 14). In the ripening seed the walls of the cell layers

beneath the enlarged epidermal layer become lignified and extremely hard, forming a stony layer. The flattened margin of the ovule expands into a narrow wing which is notched at the apex. The wing is often unevenly developed due to compression of the seeds in the loculus during development.

The embryo is straight, with two flat cotyledons, a short radicle and plumule (Fig. 14). A copious endosperm is present.

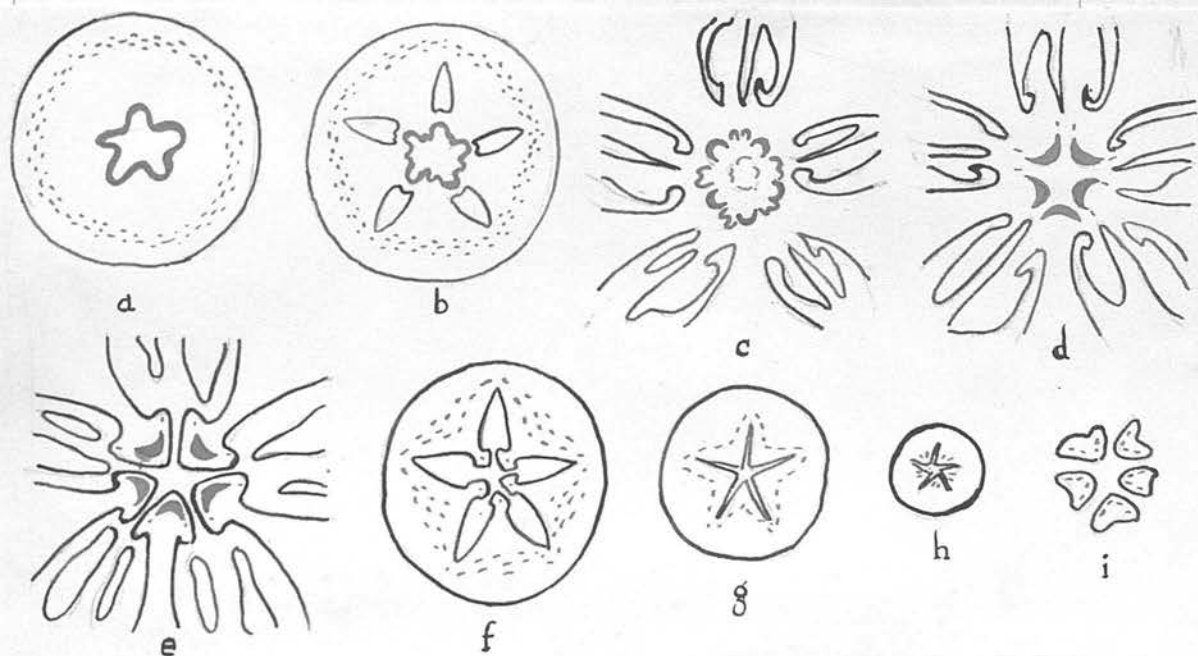
Vascular Anatomy of the Flower.



Text - Fig. 1. Vascular system of torus. Diagram.

The simple cylindrical stele of the pedicel (Text - Fig. 1a) becomes convoluted in the base of the torus and gives off numerous branching strands to the calyx (1b). The cylinder now breaks up and shows five open

'arms' of vascular tissue in T.S. At this level the petal traces separate (1c). The base of the calyx, containing numerous small strands, now becomes distinct, though not yet separate from, the torus. The petal traces reach the edge of the torus. The central stele now consists of five large open 'arms' or rays of vascular tissue, joined at the centre (1d). At a slightly higher level (1e) the calyx separates and the five stelar arms begin to branch and spread out at their extremities, giving rise to numerous stamen traces which become arranged in two concentric rings in the base of the staminal tube which soon separates together with the petal bases (1f). The remaining vascular tissue supplies the ovary. The five arms again give rise by branching to numerous strands in the outer part of the ovary wall. The remaining central stele diminishes to a small five-lobed cylinder (Text - Fig. 2a).



Text - Fig. 2. Vascular system of Ovary. Diagram

The central cylinder becomes more convoluted at the level of the bases of the five loculi (2b). Ten lobes separate from a small central residue which soon disappears (2c). The five largest strands alternate with the loculi, (i.e. they are the fused marginal strands of adjacent carpels). Each of the five smaller strands opposite the loculi splits into two small strands which soon disappear (2d). The carpel margins now separate in the centre of the ovary (2e), bearing the ovules on their recurved edges and each with a single vascular strand which disappears at the apex of the ovary (2f). The numerous strands in the ovary wall converge toward the centre and concentrate around the stylar canal in greatly diminished amount (2g, h) eventually ending in the stigmatic lobes.

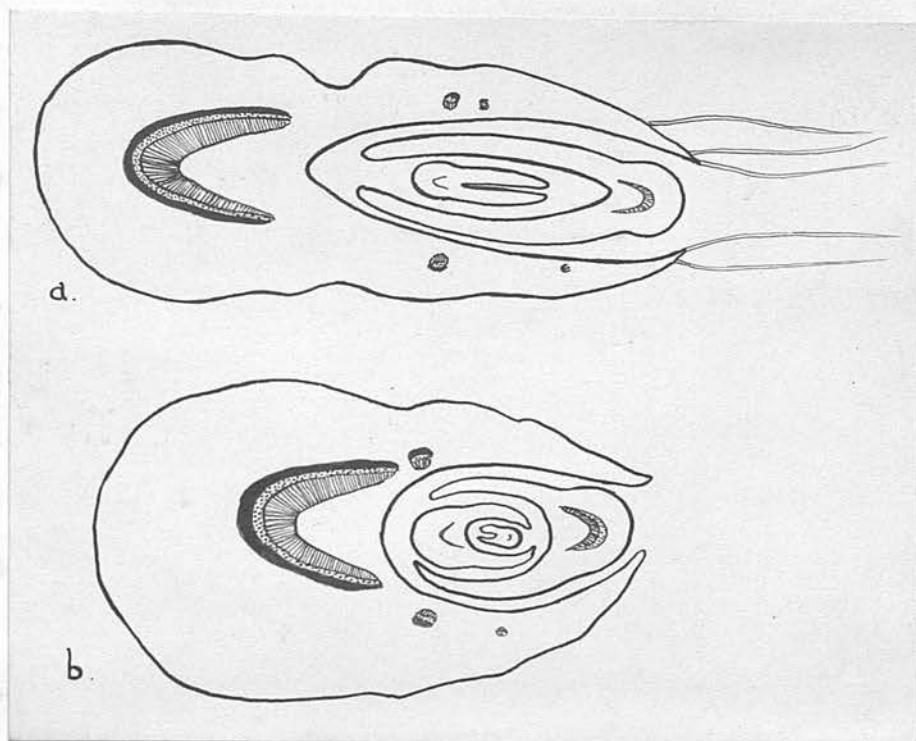
The Leaf.

The Lamina. The simple hairs which are sparsely scattered over the lower surface are unicellular with thick walls and a bulbous base in the palisade layer. They originate in the young leaf from a single cell in the sub-epidermal layer at the stage when this layer is beginning to differentiate as the palisade (Fig. 17).

The internal structure of the lamina is that of a typical unspecialised dicotyledonous leaf and shows no striking anatomical features. The cells of the upper epidermis are wavy in surface outline (Fig. 15),
of and
isodiametric, / average diameter 16μ / depth of 6μ . A

thin cuticle is present. The lower epidermis is similar except that it contains numerous stomata (average density 15,000 per sq. cm. of surface) which are evenly distributed and show no special orientation with regard to veins or midrib. Guard cells average 6-10 μ in length, 4 μ in diameter, with a pore of 3 μ diameter, and are surrounded by five or six normal epidermal cells (Fig. 16). The single palisade layer occupies barely $\frac{1}{3}$ of the total thickness of the mesophyll (Fig. 17); the remaining $\frac{2}{3}$ is due to mesophyll tissue with intercellular spaces and sub-stomatal cavities. Clustered crystals of calcium oxalate occur sparingly. The small lateral veins run through this tissue; they are without bundle sheaths and have associated secretory cells whose contents stain readily. The midrib also has no accompanying sclerenchyma. In T.S. the single bundle appears as an upward-curving arc. Some of the cells immediately below and above the bundle contain darkly-staining products of cubical, rhomboid or irregular shape which may be secretory or excretory in nature. Numerous crystals are present in the midrib parenchyma.

The petiole of *Hartia* is interesting in that it is extended into two 'wings' which completely enfold the bud and, in the case of the terminal leaf, the growing point of the stem. The peculiar petiole is the only really constant character distinguishing this genus from the closely similar genera *Stuartia* and *Schima*.



Text - Fig. 3. Leaf bud within petiole. T.S. x 20

a) centre of petiole.

b) base of petiole.

The petiole is clothed with a silky grey pubescence which is longest along the edges of the wing-like extensions. The first leaf of the bud encloses within its folded lamina (Text - Fig. 3a) and winged petiole (3b) the next young leaf, which in its turn enfolds the next, and so on.

The extension of the petiole into two 'wings' has necessitated changes in internal structure. Mechanical support is attained by the development of a narrow band of sclereids and stone-cells along the inner side of each wing (Figs. 19, 20). The large vascular strand takes the form of a deep V in T.S., the edges of the V being almost co-extensive with the ends of the

strengthening bands supporting the wings. Xylem is strongly developed and the whole strand is surrounded by a sclerenchymatous sheath. A few small lateral strands branch into the wings from the main vascular trace at the base of the petiole. The main body of the petiole consists of loose parenchyma containing numerous chloroplasts, and clustered crystals in the region of the vascular bundles. Crystals are especially abundant immediately below the main vascular strand (see Fig. 20).

The leaf trace leaves the stele as a simple up-curved strand which becomes more indented to form a V on entering the base of the petiole.

The Stem.

The young primary stem shows a wide cortex, a ring of small protophloem-protoxylem groups of indefinite number and a large pith. The epidermis consists of very small cells; underlying it is a hypodermal layer of rather large cells.

Both cortex and pith consist of large, colourless parenchyma cells intersected by a network of smaller, photosynthetic cells containing chloroplasts (see Fig. 21). This type of tissue was termed "reticulately heterogeneous" by Solereder (1908) who recorded its occurrence in the pith of *Stuartia* species. Clustered crystals are present in cortex and pith, in both types of cell.

Secondary growth begins at a short distance behind

the growing tip. The formation of inter-fascicular cambium links up the small groups of primary vascular elements, and subsequent division of the cambium cells produces a ring of secondary xylem and phloem around the pith. Cells of the pericyclic region immediately external to the phloem differentiate, by thickening and lignification of their walls, into a continuous ring of sclerenchymatous fibres (see Fig. 21).

The young stem is often somewhat flattened and appears oval in T.S. (Fig. 21), due to an unequal development of the secondary xylem, which is produced in greater amount at one side than the other. The enlarged xylem region consists chiefly of vessels, whereas the remainder of the first-formed secondary xylem consists solely of small prosenchymatous elements.

Bark formation. With rapid increase in volume of the stele, due mainly to the production of secondary xylem, the primary epidermal and cortical tissues rupture and scale off as the first bark (Fig. 22.). The secondary bark thus consists solely of cork, which originates within the pericycle, and the secondary phloem.

The secondary phloem consists of wedge-shaped masses of phloem tissue separated by the broadened extremities of numerous medullary rays (Fig. 23). The former is composed of sieve tubes, companion cells and associated parenchyma intersected by narrow and often irregular tangential bands of lignified fibres.

Secondary xylem. The wood is hard and of an even texture. The numerous vessels give it an open appearance in T.S. (Fig. 24) but individually the vessels are of small diameter ($20-40\mu$). The limit of annual growth is marked by a narrow ring of small, tangentially-compressed prosenchyma. The vessels are not disposed in any regular pattern but are evenly distributed amongst a ground mass of prosenchymatous elements and xylem parenchyma which is intersected by numerous medullary rays. The vessel segments are long (about 140μ) and the septa sharply oblique. Bordered pits on the vessel walls are oblong in surface outline, showing a tendency to become reticulate.

The prosenchymatous elements are of small diameter ($15-30\mu$); in vertical length they vary from $90-120\mu$ and have tapering ends. Xylem parenchyma is both para- and metatracheal in position, chiefly the latter.

The medullary rays are numerous and narrow, often appearing uniseriate in T.S. In L.T.S., however, they are seen to be heterogeneous (Fig. 25). The end cells of the ray are tapering.

DISCUSSION.

The Flower. In the arrangement of its parts the flower of *Hartia* closely resembles those of the genera *Stuartia* and *Schima*. Features common to all three genera include the flowers usually solitary in the leaf axils, the numerous stamens joined to the corolla at their base, versatile anthers, a normally five-locular ovary and flat winged seeds. The flower of *Hartia* differs from that of both *Stuartia* and *Schima* only in the greater degree of cohesion of the stamen filaments and the presence of copious endosperm in the seed. It differs from *Stuartia* in the presence of four ovules in each loculus of the ovary and in the simple style (the latter genus possessing only two ovules in each loculus and five free styles); from *Schima* in the erect ovules and always solitary flower (the latter has pendulous ovules and a short racemose inflorescence in some species).

Dunn (1905), in his original generic description of *Hartia*, noted that it was "distinguished from *Stuartia* by a greater cohesion of the stamens and more numerous seeds, and from *Schima* by greater cohesion of the stamens, acuminate fruit, copious albumen and straight embryo". Chun (1935) however, stated that "the only real distinction lies in the cymbiform petiole which enfolds successive growing points. Other distinctive characters enumerated by Dunn (i.e. greater cohesion of

stamens and more numerous seeds) are only relative - in Schima the filaments may vary from entirely free to one-third connate, and the number of ovules in Stuartia, although usually two and collateral, may be four and superposed as in Hartia, in some species". Dunn's comment was made with knowledge of only the one species, Hartia sinensis, Chunn's with access to material of several additional species and is no doubt the more correct.

It would appear, therefore, that there is no constant floral character distinguishing Hartia from Stuartia and Schima, apart from the presence of copious endosperm in the seed.

The Vegetative Organs. Little information is available on the anatomy of related genera, so that a detailed comparison of their vegetative structure with that of Hartia is not possible. The Ternstroemiaceae does not, as a whole, show any outstanding anatomical features common to all or many of its constituent genera. It may be said, however, that in its internal structure Hartia combines several features of the genera Stuartia and Schima, although it is lacking in others. Compared with the former genus it shows a similar structure of the pith and place of origin of the cork. It agrees with Schima in the presence of a complete ring of pericyclic sclerenchyma in petiole and stem and numerous bast fibres in the secondary phloem. It differs from both genera in the total absence of

sclerenchyma from the leaf lamina. Sclereids are a characteristic feature of the mesophyll of many genera of the family.

Wood structure in the Ternstroemiaceae has so far received little attention. No information is available on the secondary xylem of Schima, but of Stuartia Solereder (1908) states that the vessel walls show "exclusively scalariform perforations and spiral thickening" and that the medullary rays are "comparatively few". The vessels in Hartia show oblong to scalariform perforations and medullary rays are very numerous.

Conclusion.

From what has already been noted in the comparison of Hartia with the closely similar genera Schima and Stuartia it is evident that, floristically at least, Hartia holds a position very close to, if not actually intermediate to, these two genera. Anatomically its position is not so clear because of the relatively scanty information available on the vegetative anatomy of related genera. In one respect, that of the total lack of sclerenchyma in the leaf, Hartia differs markedly from both Stuartia and Schima. Since, however, vegetative structure within the Ternstroemiaceae is very varied, anatomical characters being of use only in specific diagnosis, it is to be expected that the genus Hartia would not show any marked similarity with allied genera.

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HARTIA SINENSIS Dunn.

FIGURES.

Fig. 1 Inflorescence. Slightly less than natural size.

Fig. 2 Flower. Vertical section X 2.
showing reflexed perianth and erect staminal tube.

Fig. 3 Fruit and seed X 1.
Note persistent calyx.



Fig. 1

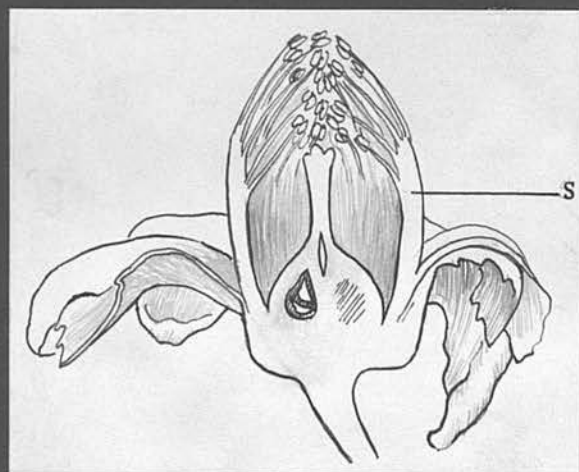


Fig. 2

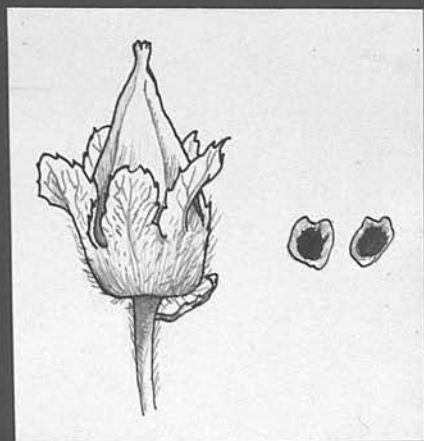


Fig. 3

Fig. 4 Floral diagram.

Fig. 5 Flower bud. T.S. X 10.

Note large posterior petal (p) enclosing the other petals.

Fig. 6 Stamen X 10.

Only the free upper portion of the filament is shown. Note central attachment of anther.

Fig. 7 Mature anther. T.S. X 40.

s stomium

Fig. 8 Stomium of anther. T.S. X 120.

showing strengthening bands of cells of stomium and endothelial regions.

Fig. 9 Dehiscid anther. T.S. X40 .

Fig. 10 Stigmatic lobes. T.S. X 20.

Showing conducting tissue (c) on inner surfaces.

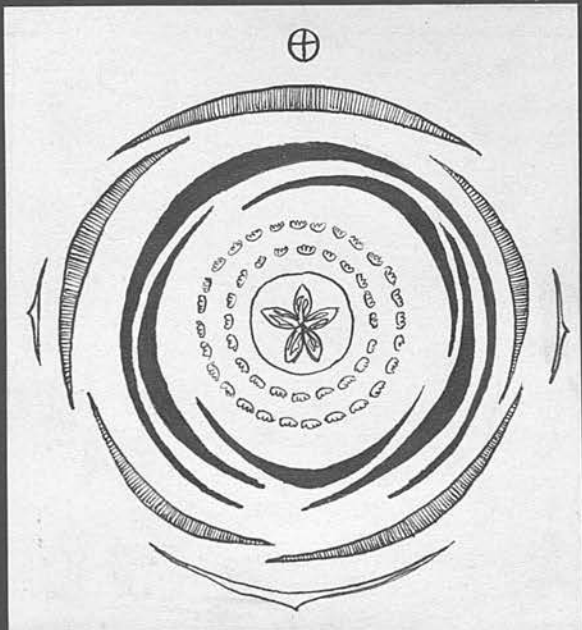


Fig. 4

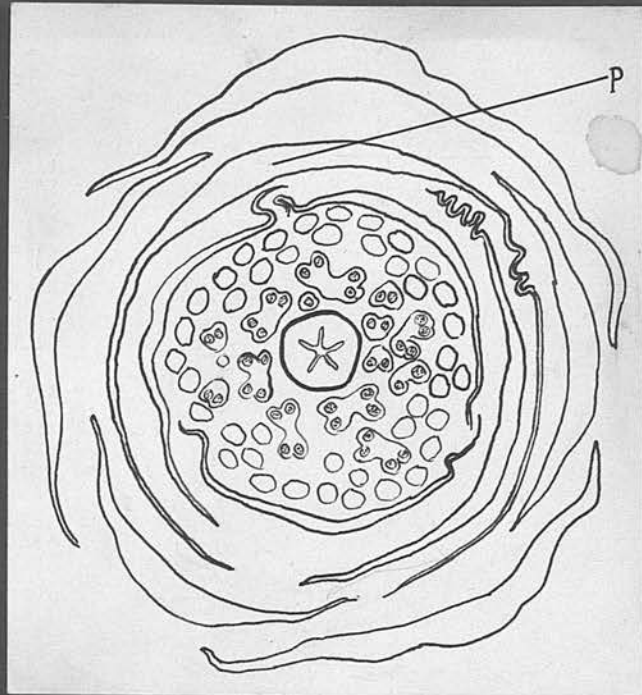


Fig. 5

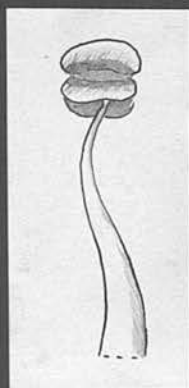


Fig. 6

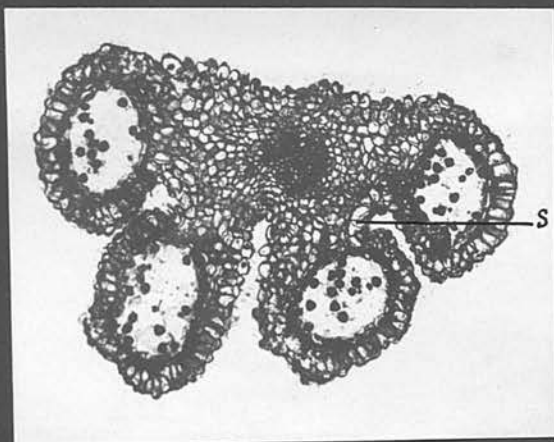


Fig. 7

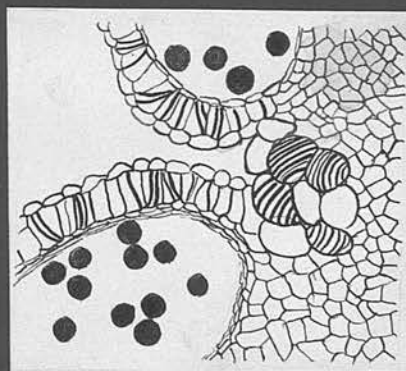


Fig. 8



Fig. 9

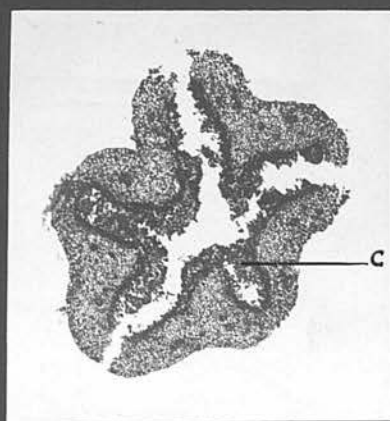


Fig. 10

Fig. 11 Ovary. T.S. centre X 25.

showing separation of carpel margins.

Fig. 12 Ovule. T.S. X 50.

Detail of Fig. 11.

es large embryo sac
n abundant nucellus
ep prominent epidermal layer
m flattened margin

Fig. 13 Developing seeds. L.S. X25.

showing superposition of ovules in loculus,
and densely-stained secretory cells in the
central axis.

Fig. 14 Developing seed. T.S. X 30.

Note flattened margin (m).

Fig. 15 Upper epidermis of leaf. Surface view X 400.

Fig. 16 Lower epidermis of leaf. Surface view X 400.

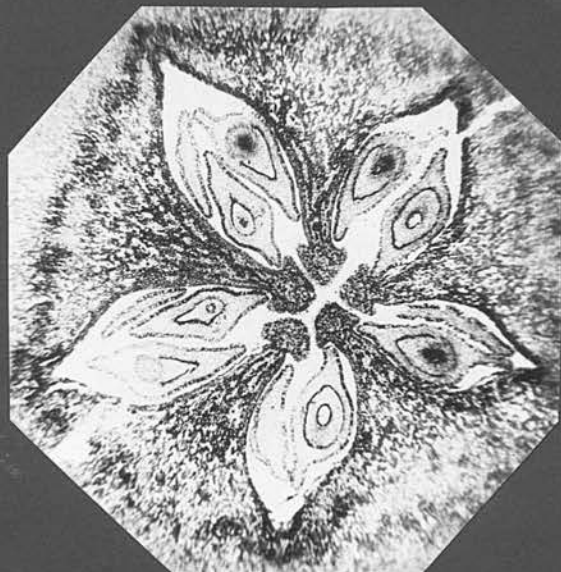
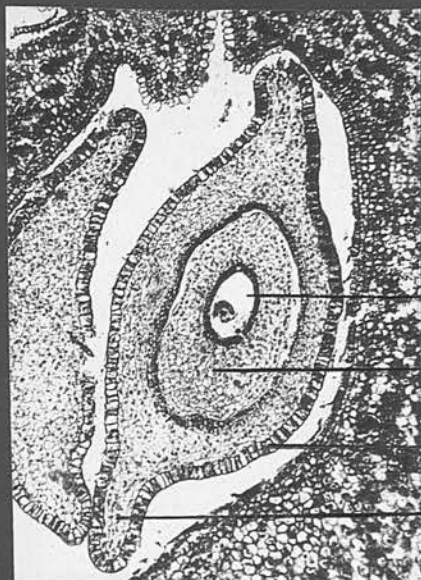


Fig. 11



es

n

ep

m

Fig. 12



Fig. 13



m

Fig. 14

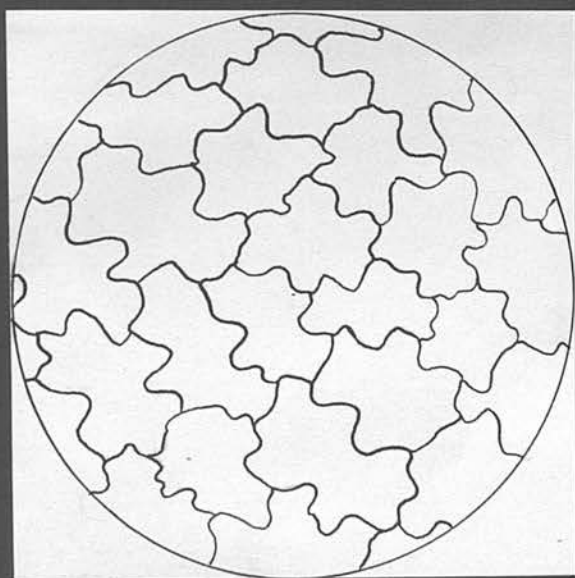


Fig. 15

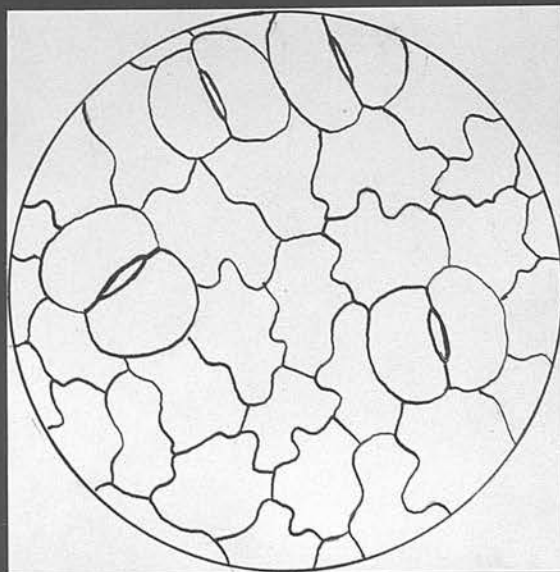


Fig. 16

Fig. 17 Young leaf tip. T.S. X 300.

showing base of hairs in the sub-epidermal layer.

Fig. 18 Leaf lamina. T.S. X 300.

showing lateral vein and clustered crystal in the mesophyll.

Fig. 19 Petiole. T.S. X 25.

s band of sclereids and stone cells
lb lateral bundle
vb main vascular bundle
c clustered crystal

Fig. 20 'Wing' of petiole. T.S. X 100.

ue upper epidermis
s sclereids and stone cells
le lower epidermis

Fig. 21 Young stem. T.S. X 25.

showing uneven development of secondary xylem and a heterogeneous cortex and pith.

c crystals in cortex and pith
s pericyclic sclerenchyma

Fig. 22 Secondary stem. T.S. X 25.

showing two years' secondary growth and loss of the first bark.

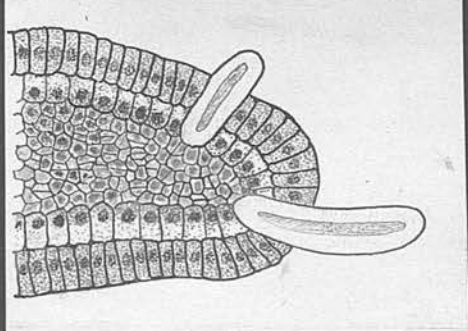


Fig. 17

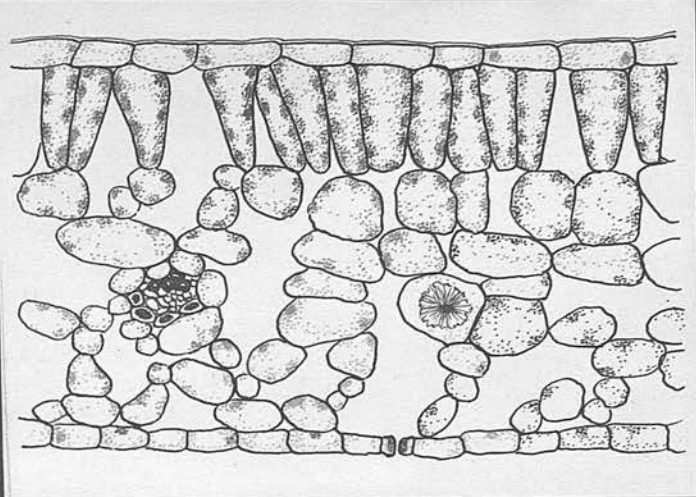


Fig. 18

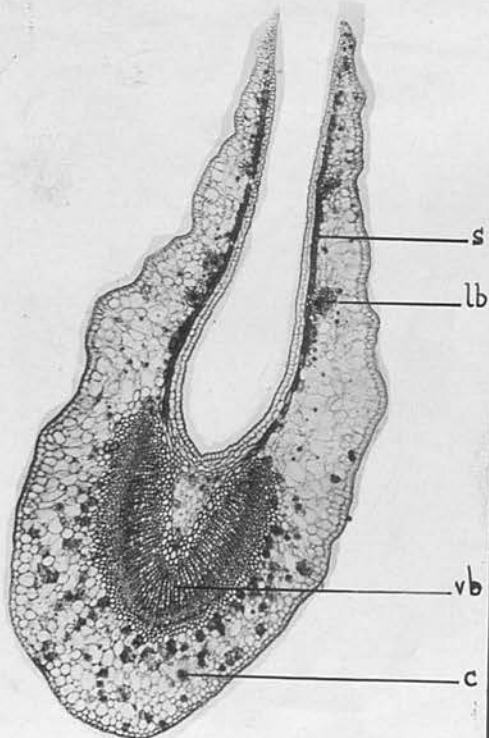


Fig. 19

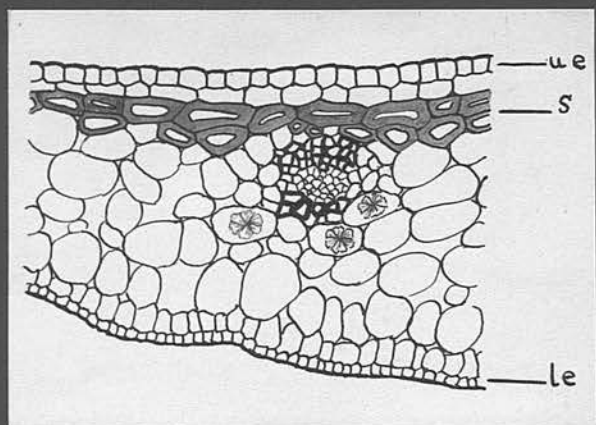


Fig. 20

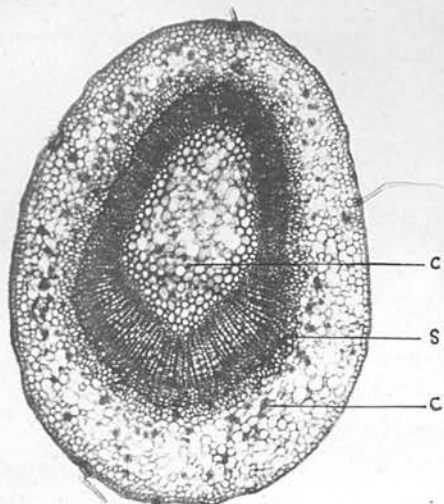


Fig. 21



Fig. 22

Fig. 23 Secondary phloem. T.S. X 50.

c cork
mr broadened extremity of medullary ray
ph wedge-shaped mass of secondary phloem
wc wood cambium

Fig. 24 Secondary xylem. T.S. X 40.

Fig. 25 Secondary xylem. L.T.S. X 50.

showing heterogeneous medullary ray and
abundant xylem parenchyma.

Fig. 26 Secondary xylem. L.R.S. X 50.

showing heterogeneous ray.

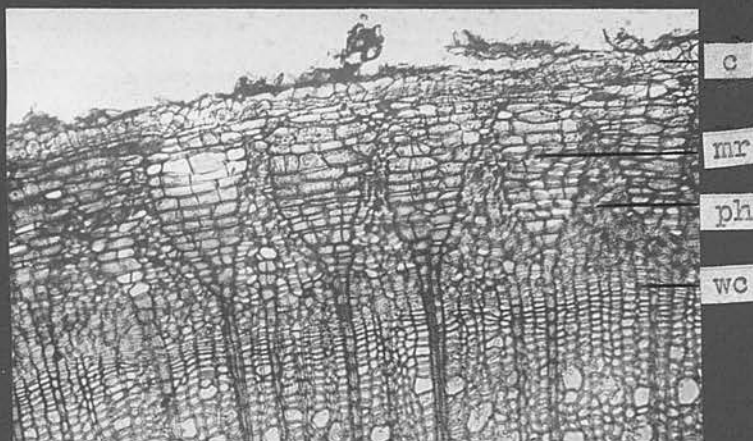


Fig. 23

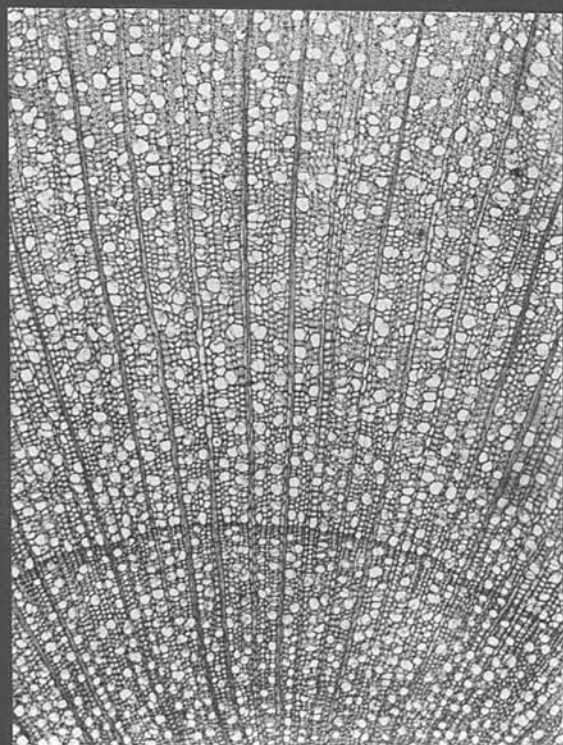


Fig. 24

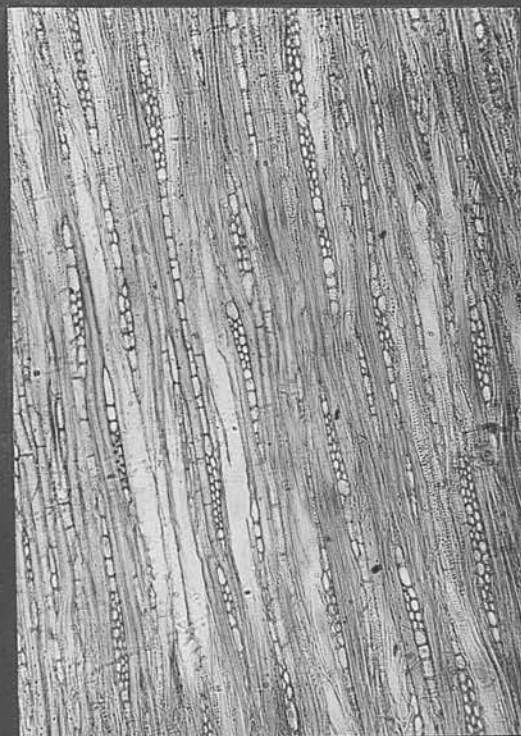


Fig. 25

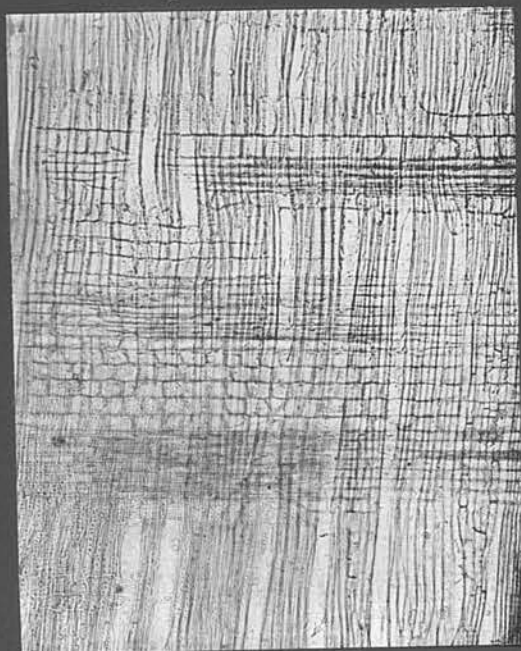


Fig. 26